AN INTRODUCTION TO ZOOLOGY

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BY

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PREFACE

THE object of this volume is to provide a text-book for the zoological portion of the syllabus in Biology for the First Examination for Medical Degrees of the University of London, and the First Examination for the Conjoint Examining Board in England of the Royal College of Physicians of London and the Royal College of Surgeons of England. Some years' experience in preparing fairly large classes of students for the above examinations made quite clear the need for such a text in spite of the text-books of Zoology available. It is based on the lectures then given, and its method of treatment is that found to suit the needs of the students. It is hoped that it will also prove useful to students preparing for similar examinations of other British Universities, and for those who are taking classes, like the premedical courses in American Universities, requiring a knowledge more particularly of Vertebrate Zoology.

The above requirements have naturally determined in the main the types studied, but the syllabus has not been slavishly followed in places where it was considered the student would benefit by considering examples outside it. Types like the Crayfish, *Astacus*, the Fresh-water mussel, *Anodon*, and the Cockroach, *Periplaneta*, often included in elementary books, have been omitted. This was done because it was felt that the knowledge of such specialised types, while essential to a student proceeding with the more advanced study of Zoology, involve a great deal of detail unnecessary from the point of view of students proceeding with medical studies, and, moreover, they do not illustrate any fundamental principles that cannot also be dealt with in connection with the types chosen. The space so gained has been utilised to describe fairly fully the structure of a mammalian skull, that of the dog, of a mammalian heart, that of the pig or sheep, and of a mammalian brain, that of the sheep. While the detail in these cases is perhaps rather more than required for examination purposes, it is hoped that their study will be of value in the subsequent work in Anatomy. Then, too, Cytology, Histology, and Embryology have received fuller treatment than is usually the case, since they are subjects of importance in future

studies. Finally, the last chapter has been devoted to an introductory outline of the principal theories concerning Heredity, Variation, and Evolution. This chapter does not pretend to completeness, for the treatment of this even in an elementary way would require a large volume in itself. It is treated in a historical manner and intended as a preliminary to wider reading, much of which is of importance in the practice of medicine and should be included in any curriculum of education. The many excellent books now available on these topics almost all assume implicitly or explicitly such information as this chapter contains.

In arranging the book the plan has been followed of first treating the frog fully as an introduction to morphology, physiology, and histology, and then starting with the Protozoa and working up to the higher forms. This has been done not because it is perhaps the traditional method in England since Huxley's time, but because actual experience of other ways has shown it to be the most satisfactory both from the point of view of the teacher and the student. The arrangement of the book, however, allows of almost any alteration in the order in which the forms are studied. As the medical student is going on to what is and must be a highly technical training, no attempt has been made to avoid technical terminology, although in all cases where such terms are used they have been defined and also printed in thicker type to facilitate ready reference. No course in Zoology can be considered as adequate unless the reading is accompanied by a satisfactory practical course, and this has been borne in mind in choosing the illustrations. Certain portions are better illustrated by the practical work itself, while others need fuller illustration in the text.

I have to thank the following publishers for permission to use the following illustrations :—

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To my colleague, Mr. William Rowan, I am indebted for the originals of figures 3, 4, 6, 7, 91, and 93. The remaining figures have been drawn for this work from preparations or from the original papers. My former colleague, Dr. Katherine M. Parker, kindly read through much of the manuscript of the early chapters. Messrs. Bell and Sons, the publishers, have given me much assistance and consideration. Lastly, my wife has helped me in many ways, not the least of which was the preparation of the index. To all of these I wish to express my sincere gratitude and thanks.

In spite of good intentions, errors have doubtless crept in, and I should be glad if these are brought to my notice.

The book is for the use of students, most of whom will be pursuing courses in allied sciences, and I trust that they will be able to obtain from it a sound introduction to Vertebrate Zoology, and some knowledge of and interest in the general principles of that science. Much of any good it may contain is due indirectly to the excellent courses given by Professor A. Dendy, F.R.S., and Professor J. P. Hill, F.R.S., of the University of London, to both of whom the author is deeply indebted. In the case of Professor Hill, moreover, my indebtedness is more direct, since, for several years, I was in charge of the practical classes accompanying his lectures, and so had an opportunity of becoming familiar with them. This was of considerable advantage to me in preparing the book, parts of which are more or less directly based upon his lecture-notes; and I desire, therefore, to express to him my sincere thanks.

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UNIVERSITY OF MANITOBA,
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AN INTRODUCTION TO ZOOLOGY FOR MEDICAL STUDENTS

CHAPTER I

INTRODUCTION

THE many things that we encounter in our everyday life we soon learn to divide into two more or less sharply contrasted groups, the living and the non-living. This classification is a fundamental one, and when we come to the Sciences, that is, the ordered and intensive study of these things with a view to understanding them and explaining them, we find that they also fall into two corresponding fairly distinct categories, the **Physical Sciences,** treating of non-living things, and the **Biological Sciences,** concerned with living things. The two groups differ not only in their content, but, as the nature of this is dissimilar, the methods in which they can be investigated, that is to say, the **technique**, is also different in the two cases.

Biology is the branch of science that treats of living things in their manifold relations with one another and with non-living things. Living beings are generally recognised as being divided into Plants and Animals, and while, as a matter of fact, we find a certain amount of overlapping between the two when we study them in detail, this is a moderately clear cut division, to correspond with which Biology may be subdivided into **Botany**, the study of plants, and **Zoology,** the study of animals. The present book is concerned with the latter, namely Zoology, or more accurately with some aspects of it as illustrated by certain type forms treated in an elementary manner.

The field covered by Zoology is so vast that it is necessary to split it up into a number of daughter sciences. These fall under two fairly general headings, according to the point of view adopted in making our study. In the first place, we may be concerned chiefly with the questions of the structure of animals, this is termed **Morphology,** and in the second we may consider in the main the various activities manifested by animals, and this is **Physiology.** The two require different techniques, but, for the satisfactory

investigation of either one, it is necessary to take into consideration the other, and so they are, or should be, to a considerable extent complementary.

These two main divisions are sub-divided, as has been indicated. In Morphology we may consider the general external form, number of parts, their relation, size, etc., and this is distinguished as **gross Morphology.** We may also examine the actual parts, both internal and external, of an animal, their general structure, relation to one another, and to the body as a whole. This we term **Anatomy,** and as a rule it necessitates the use of scalpels, scissors, etc., to dissect the various structures. When this is done we may pass on to consider in detail the manner in which the various parts are built up, a branch of enquiry termed **Histology,** and requiring for its pursuit a microscope, microtome, etc. This reveals the fact that the whole of an animal's body is composed of, or has been derived from, a series of tiny vital units termed **cells,** and the further more intensive study of these minute particles is termed **Cytology.** Again, all animals commence life as a small portion of living matter known as an egg, a fact that is common knowledge in the case of birds, butterflies, flies, etc., and we are confronted with the problem as to how this comparatively simple body becomes a complex adult animal. This is a branch of enquiry known as **Embryology,** the study of development.

Underlying all sciences are certain fundamental beliefs, and the two most important of these, in the case of Zoology, are the **Uniformity of Nature** and **Evolution.** The first of these implies that the various forces that we can see operating in Nature to-day have been in action in times past, and will go on in the future, although it may be that individual forces have varied somewhat in intensity or point of application at different times, and may do so again. By Evolution we mean that the various living forms that we know to-day are directly derived from those that have gone before, and that in turn they will give rise to those that are to come. Their diversity is due to the continuous interplay of the forces included in the first, acting upon and modifying successive generations of living beings. It should be borne in mind, however, that these beliefs do not imply an act of faith, but are simply generalised statements of observations that have not been contradicted by experience. As an outcome of the last, it follows that the various animals are related to one another in different degrees. The last branch of Morphology concerns itself with expressing these relationships as accurately as our knowledge allows, by classifying and arranging animals in groups and systems of groups, and when this is done they are given names indicating, to a certain extent, their positions

in such a scheme. These two branches are closely allied, and are termed **Classification** and **Taxonomy**.

Physiology, as has been noted, deals with the activities or functions of animals, and falls into three main divisions. The first of these is **Ecology** or **Bionomics**, that is to say, the study of the activities and responses of an animal in its natural surroundings, and its relation to other animals, inanimate things, and conditions. This in a way resembles gross morphology, since it requires the use of no special instruments or technical appliances, and as it is not suited to laboratory study is unfortunately omitted from most courses.

Secondly, we can investigate the activities of an animal or its parts under experimental conditions, testing and measuring them in various ways, and so employing apparatus of a physical nature; this we usually term **Experimental Physiology.** A further interesting branch of biology most closely connected with this is **Experimental Psychology,** which is the study of the responses that an animal is able to make by reason of its possessing a distinct nervous system, and hence in the higher forms often described as a study of the mind.

Thirdly, the functions of an animal may be approached from the chemical point of view, and their chemical antecedents and results investigated; this is termed **Chemical Physiology,** and, as will be seen, requires the apparatus and methods of the chemist.

A last branch, which although sometimes considered as separate, is nevertheless closely bound up with the first of these, is **Distribution.** It is obvious, of course, that the reactions of an animal, to a large extent, determine where it is possible for it to live and its activity, whether or not it can spread widely. Distribution itself has two distinct aspects: **Geological Distribution,** *i.e.* distribution in time, and **Geographical Distribution,** *i.e.* that in space.

All these various branches of zoology have been concerned with the acquisition and verification by various ways and means of all the many facts relating to animals. Finally, we have left the branch of that science that deals with the correlation of these facts, their reduction to a state of order and arrangement in systems, and further endeavours to ascertain the causes responsible for their production, and to give explanations of the manifold phenomena. This branch, which rounds off the others and borrows extensively from all other sciences, is termed **Aetiology,** and obviously it is closely concerned with evolution.

We may divide up the study of Zoology into these various aspects for the sake of clearness in arranging our ideas, but any piece of zoological work cannot be confined to just one of them, it must involve two or three, at any rate, and probably more.

Before leaving this question of classification we may glance at the somewhat misleading way in which the terms are ordinarily applied in Universities and Colleges. Owing to the importance of one animal, Man, and the fact that a medical training is intended to give the student some detailed knowledge of this species in particular, it is customary to take the general terms Anatomy, Histology, Physiology, etc., and apply them to Man. They would be more accurate if they had prefixed to them the word Human, and so read Human Anatomy, etc., as is sometimes done. Then, too, in the case of the terms Biology, Zoology and Botany, it is obvious that a junior student cannot be expected to know the whole of the ground covered by any one of these. So the terms come to be used as convenient ones for indicating courses of study that endeavour to give, often by the utilisation of certain types, an introduction to the elementary fundamental ideas underlying the Morphology, Physiology and Aetiology of animals or plants, or both.

Life.

We have spoken of the division of material objects into living or **animate** and non-living or **inanimate,** and it is necessary to consider further what we mean by the word "living." Living things are characterised by the possession of "life," and, furthermore, we only know of "life" as a manifestation of such beings. It is a matter of great difficulty to give a concise and satisfactory definition of life, although we all of us know more or less clearly what it implies, and it is brought most strikingly to our notice when it ceases, and a living being becomes dead.

It is unnecessary to attempt to define life, since for our purposes it will be sufficient to become familiar with its more important manifestations which we distinguish as vital phenomena, some of the most obvious of which we make use of in determining whether a thing is alive or lifeless. The most striking are those that concern the activities of living things, and so fall under the heading of physiology.

Irritability.

If we poke a stone that is firmly seated nothing happens, yet, on the other hand, if we perform the same experiment on a living animal it would most probably make some movement in reply, the nature of the reply depending on the animal. Here, in a crude way, we have utilised one of the characteristic vital activities to determine whether a thing is living or not, and we shall consider briefly what it involves. In the case of the stone nothing happens,

because, as we put it in everyday language, the stone cannot "feel." Any force, mechanical, electrical, or heat change, light change, gravity, and so on, that can in any way effect an organism we speak of as a **stimulus.** The animal, then, has a means of appreciating stimuli, and this is true also of plants. We can test this very readily if we put a living plant near a window, when we shall find that the growing parts turn towards the light, the plant then can appreciate the stimulus of light. A second factor is also involved in the initial experiment, and that is that not merely is the stimulus received, but a reply is made to it, and still further, the reply is generally a fitting one. Here, then, we have had an illustration of a fundamental vital phenomenon, namely, the power of making a response, usually a suitable one, to a stimulus, and we term this attribute **Irritability or Sensitivity.**

Any particular living being occupies a characteristic situation or, as we say, **habitat,** where it is constantly subjected to a stream of typical stimuli reaching it both from within and without. The whole of the stimuli that affects an organism from birth to death we can conveniently include in the one term **Environment.** It is obvious, on reflection, that the nature of the habitat determines to a large extent the environment. Thus, for example, it is clear that the stimuli affecting an animal like a fish living in the water are different from those reaching an air-dwelling form like a bird. Moreover, while both may have a number of stimuli in common, such as external temperature changes, or internal feelings of hunger, and so on, each is subjected to stimuli peculiar to its habitat, and not playing upon the other, so that each comes under the influence of a different and characteristic environment. Again, when we consider the response that is to be made to these manifold stimuli, we shall see that in order to live an animal or plant must reply in such a way as to preserve its life in its environment. Hence, this power of irritability is not only a fundamental characteristic of organisms, but within certain limits an absolutely essential one for self-preservation.

Metabolism.

It is a matter of common knowledge that living beings require food in order to live, and the nature of this food and the manner in which it is dealt with constitute the second of the vital phenomena. While an inorganic body, such as a crystal, is able to increase in size or grow, it can only do so when it is provided with a substance that is chemically similar to itself. On the other hand, an organism is able to utilise materials unlike itself for food, and from them to build up its own substance. This is a capability

that we term the power of **nutrition,** and it always involves certain subsidiary processes. Just as a fire needs a constant supply of fuel, so an organism must have food to maintain its vitality. Plants in general grow in such situations that they can obtain their food from the water, the soil and the air surrounding them, and so are fixed, whereas animals usually have to seek out their food, and are, in consequence, able to move from place to place. The food, when it reaches the organism, is taken in or **ingested** in some way or other, and this is the first process of nutrition. Many of the substances ingested can be dealt with straight away, because they are soluble, but a number of others are insoluble or unable to pass into the living substance until they are altered in some way or other, usually, in the case of animals, reduced to more simple compounds. This, then, is the second process of nutrition, namely, **digestion,** or the changing of the chemical nature of the food in such a way that it can be taken up into the organism. The third step consists of the building up of these substances, chemically speaking, relatively simple, into the complex compounds characteristic of living beings, and this is termed **assimilation.** Lastly, in order to obtain the substances required as food, it is nearly always necessary to take in certain other materials that are not wanted, and often, too, materials that cannot be rendered soluble by the process of digestion. This is noticeably the case in animals, and we find this waste, or better, not-utilisable matter, voided from the body as fæces, a process termed **egestion**.

This is, as it were, the " receipts " side of the account of living matter, and it results in the replacement of used-up material, and perhaps an increase in size or growth or a storage of certain reserve food substances until such time as they may be required. To one part of this, namely, the building up of the living matter or **Anabolism,** we shall return later when we have considered this substance from the physical and chemical points of view.

On the other hand, we have also to consider the " expenditure " side of the account. In order that these complicated chemical changes may go on, it is necessary for the organism to obtain Oxygen, and this it gets, as a rule, from the air or water surrounding it by a process termed **Respiration.** Again, just as a fire requires Oxygen to continue burning, so also oxygen is a necessity to living matter, and a further parallel between the two can also be drawn. The burning of the fire results in the formation of various waste matters, taking the form of gases and ash. The activities of an organism also produce waste products. One of these is the gas Carbon Dioxide, and quite frequently the same mechanism that serves for obtaining the oxygen supply is also utilised to get rid of

the carbon dioxide. This is particularly the case in animals, and the term respiration is most frequently used to imply this exchange of carbon dioxide for oxygen. The other waste products, corresponding superficially to the ash of the fire, cannot be eliminated in this way, and the process of removing them is termed **excretion.** This getting rid of the substances resulting from the break down of living matter, *i.e.* excretion, must be carefully distinguished from the removal of the insoluble material taken in with the food, but never at any time forming an actual part of the organism. These breaking down processes are collectively termed **Katabolism.** The power to carry out the constructive and destructive changes, together included in the term **Metabolism,** constitutes the second of the fundamental vital phenomena, and we shall investigate this matter more fully later after a fuller examination of the nature of the living substance.

Growth and Reproduction.

The organism, then, is the seat of two antagonistic processes, anabolism and katabolism. If the two are about balanced a condition of relative stability is attained, whereas if the former is in excess of the latter, then an increase in size or, in other words, growth takes place. The growth is of a peculiar form, for the new material is added in extremely minute particles throughout the whole of the living substance, a process termed growth by **intussusception.** A crystal, on the other hand, even if it does increase in size, does so by the deposition of layers upon its surface ; this is growth by accretion. The former variety is definitely characteristic of living things.

In lower forms of animals, when they reach a certain size, determined probably by physico-chemical requirements, they divide into two separate daughter organisms, each of which, in the presence of an adequate food supply, proceeds to grow until it reaches a maximum size. Thus it will be seen that from the one original animal two have been produced, in other words, **Reproduction** or **Multiplication** has taken place, and, further, it is clear that in such cases we can regard it as discontinuous growth. All organisms possess this power of reproducing their like, although it is not always so clearly a case of discontinuous growth. In higher forms two parent individuals are concerned, termed respectively the male and the female, each of which produces as a part of itself a tiny particle of living matter, the male or the female **germ cell.** These two germs unite, a phenomenon known as **fertilisation,** and from their union a single body results that will grow up like its parents in all essential respects. Such a process is not met with

in the inorganic world, so that in this power of being able to reproduce their like living things differ from the non-living, and so it constitutes a further vital characteristic.

It has just been noted that in higher forms the union of a male and female germ cell gives rise to a new individual which undergoes a series of changes, often quite complicated, whereby it grows more and more like its parent. This process we term **development,** and it is usually accompanied by a marked increase in size or growth. It is then a period when anabolism is in excess of katabolism. At the conclusion of this period the animal is full grown, and the two processes approximately balance. Somewhere about the same time the animal becomes **adult,** that is to say, it is able in its turn to produce germ cells, and so in conjunction with another animal of the opposite sex give rise to number of new individuals. After a longer or shorter period of adult life the katabolic processes exceed the anabolic, with the result that, even if no accident or illness supervenes, there finally comes a time when some part of the organism that is of vital importance gives way, and the animal ceases to live, or as we say, dies. Death is the normal termination of this series of events, just as much as birth is its beginning. We see, then, that an animal goes through a succession of changes, beginning in the higher forms at fertilisation, including growth, and ending with death, and somewhere between the middle and the end possesses the power of reproduction. All these phenomena together constitute an ordered whole termed the **life history** or **life cycle** of the animal, and in exhibiting this organisms differ from non-living things. We have now considered the main phenomena characteristic of life, and seen that they are expressed as the functions of living beings. They are in the main four : (1) Irritability ; (2) Metabolism ; (3) and (4) Growth and Reproduction, which are closely linked and imply a life cycle. It is now necessary to examine organisms from the point of view of their structure.

Protoplasm.

The above considerations have led us to see that there are a number of points in which the behaviour of living and non-living things differ, and the powers possessed by the former are not shared by the latter. In considering the structure, too, we shall find a striking and absolute difference. When we press our enquiries to the limit we shall find that all organisms or, at any rate, the living portions of them, are composed of a highly complex substance that is termed **Protoplasm,** that is never found in the inorganic world. This material is found wherever we find evidences of life, and it is remarkably similar in chemical and physical properties in all

animals and plants. So closely is it bound up with the vital phenomena that wherever we find life we find protoplasm, and vice versa wherever that substance is found we find manifestations of vitality. This being the case, we sometimes say the protoplasm is the **physical basis of life,** or the same idea is expressed by saying that life is a property of protoplasm. From the universality of its occurrence in organisms, and the fact that it is indissolubly bound up with vital activities, it is obvious that protoplasm is a substance of extreme importance.

It is a very difficult material to deal with chemically, because when we place it in a test tube, or submit it to the ordinary methods of chemical analysis, we at once kill it, and so are no longer dealing with living matter. Ultimate analysis shows that there is no chemical element to be found in protoplasm that we cannot also find in the inorganic world, so that we cannot regard living and non-living as two essentially different sorts of matter, but only as the same matter in different stages.

While this is true of the elements contained in the living substance, it does not hold for the compounds. Chemical analysis shows us that protoplasm is an intimate mixture of a number of different classes of compounds mainly falling under five headings, viz.: water, inorganic salts, fats, carbohydrates and proteins. Of these the first two are also met with in inorganic matter, but the last three are only found as a part of, or as the products of, protoplasm, and encountered nowhere else in nature. They are for this reason spoken of as organic compounds. Fats and Carbohydrates (*e.g.* starches and sugars) are composed of the elements Carbon, Hydrogen and Oxygen in various proportions. Proteins, the most complicated compounds that we know, always contain in addition to these elements Nitrogen, and usually several others, such as Sulphur, Phosphorus, Sodium, Magnesium, Iron, etc.

In addition to this we can ascertain by experiment that when a living being dies there is no loss of weight; a very important point, since it demonstrates that the cessation of life is not accompanied by the loss of any material substance. There is, however, a remarkable change in both its chemical and physical properties, and we must assume that this is due to a rearrangement of the composition and minute physical structure of the protoplasm, as it is not due to the withdrawal of anything tangible.

Physics teaches us that energy, which is necessary for the performance of any work, exists in two forms. Firstly, we have **kinetic energy,** the variety of energy that expresses itself in the form of motion, heat, light and electricity, and is brought prominently to our notice by its results. Secondly, **potential energy** is

energy that is, as it were, stored up waiting for some stimulus to release it. A body possesses potential energy by virtue of the previous expenditure of kinetic energy upon it. Thus, to take a simple example, if we take a weight from the floor and place it on a high shelf, kinetic energy has to be utilised to do this. While on the shelf the weight manifests no activity, but it possesses potential energy as a result of its position, and if we remove the shelf from under it this stored energy becomes released as potential energy, and the weight starts to move. The work it is capable of performing may be utilised by connecting it with a machine, or else it will be transformed into heat when it strikes the ground. In a somewhat analogous way, the complex compounds have used up a supply of kinetic energy in their formation, and under suitable conditions they can be induced to break down into simpler substances and release a certain amount of kinetic energy.

The maintenance of life and the exhibition of vital activities require the expenditure of a certain amount of energy, and this is obtained by the oxidation of certain constituent parts of the living organism itself. These compounds under suitable conditions combine directly or indirectly with the oxygen supplied by respiration and break down into simpler compounds, releasing, as they do so, the necessary kinetic energy. In many cases these break-down products are substances that are of no further use, and so need to be eliminated. The production of kinetic energy therefore is the result of katabolic changes, and it takes place throughout every minute particle of the whole of the protoplasm. This wastage needs to be made good and stores of potential energy built up for future use, and this is brought about by anabolism. Thus we see that, from the chemical point of view, protoplasm is an intensely active substance, the seat of unceasing destructive and constructive changes ; it is never quite the same for two consecutive moments.

When viewed under the microscope living protoplasm is found to be a semi-viscous, almost transparent, granular substance usually in a state of motion. When examined under the highest powers a certain amount of structural organisation can be made out, but this is relatively simple, and certainly gives no hint of its wonderful complexity.

All animals are composed of this substance. At the commencement of their existence they consist practically exclusively of protoplasm, but in the higher animals other non-living products appear as a result of its activities ; in ourselves, for example, hair, nails, and the inorganic matter of bone and teeth. Such animals do not consist of protoplasm alone, but the other lifeless substances in them have been formed by it. Then, too, we find that the

protoplasm of a complex animal is not homogeneous, but is built up of an enormous number of tiny vital units, just as a building may be composed of bricks. Closer examination shows each unit to consist of a certain amount of protoplasm containing within it a denser portion. These tiny masses we call **cells,** a somewhat misleading name. A cell then is a small portion of protoplasm surrounding a denser and more opaque nodule, the **nucleus.**

As we pass down in the animal scale we find that these cells become relatively fewer in each individual, until finally, when we come to the lowest forms, the whole creature is composed of just one cell. This single cell, however, is capable of exhibiting all the vital phenomena. We therefore find that from this point of view we may divide animals into two distinct groups: one in which the individual is composed of only one cell, these we term the **Protozoa** or unicellular animals, and the other, in which the animal is built up of a large number of cells often differing enormously among themselves in size and shape, and these we designate the **Metazoa** or multicellular animals.

Although we have not actually defined life we have enumerated certain of the functional and structural characters that mark off the organic from the inorganic world, and this in itself enables us to get a clearer idea of what is implied when we say that a certain thing is alive.

The world of living beings, of which we ourselves form an integral part, presents an infinite number of problems to the enquiring mind. So diverse and so complex are they that no one person can ever hope to master more than a small group of them. We have indicated above the various ways of approaching these questions, and also endeavoured to set out those fundamental attributes of organisms, more particularly animals, that are more or less common knowledge, and often taken for granted without further thought. The purpose of the succeeding chapters is to elaborate these two points in a more thorough and systematic way, by the examination of the main problems and the methods of treating them. To do this we shall consider in a certain amount of detail a selected number of animals differing both in structure and mode of life, and chosen with a view to emphasising the course of evolution in the animal kingdom.

CHAPTER II

THE FROG—*RANA TEMPORARIA*

Introduction—General Internal Structure—Skeletal System—Muscular System and Integument.

Introduction.

Few four-legged animals are more common or more readily obtained than the common grass frog, *Rana temporaria*. It is to be found in the damp grass in the neighbourhood of ponds and ditches in all parts of the British Isles, and is probably the only native frog. A larger form. *Rana esculenta*, the edible frog, is very abundant on the continent, and although rare in this country is not infrequently imported by dealers, and finds its way thence into the laboratory. For our purposes the differences, in the main of size and colour, between the two species need not be taken into account.

The colour of the grass frog is subject to great variation, according to the nature of the surroundings in which the animal lives, but generally the back is mottled dark green, brown and black, and the under surface is pale yellow with a few dark spots. The coloration is due to the presence in the skin of a large number of deeply pigmented cells, and the colour of an individual can be changed to suit its habitat by an alteration in the size of the coloured cells. They can each be contracted into quite a tiny spot or, again, spread out over a comparatively large area. In this way the frog is protected from its enemies, for it is able to harmonise with the ground and so escape detection as long as it remains still. It is almost equally at home on the land or in the water, and it belongs to that class of animals termed the AMPHIBIA, in order to indicate this capability of living either aquatic or terrestrial lives. Although unable to walk easily it can still get about well on land, and in the water is a powerful swimmer. The long hind legs serve as efficient swimming organs, and also for locomotion on land by means of a series of jumps. It moves freely from place to place, and so we say it exhibits the power of **voluntary movement.** The food of the frog

consists of small insects, their grubs or caterpillars, worms and slugs, which it catches by means of its tongue. The tongue is capable of being shot out suddenly to a considerable distance, and has a sticky extremity to which the prey adheres. During the winter frogs hide away in holes in the ground in order to escape the cold, not only to avoid being frozen, but also because it would be practically impossible for them to obtain food during this part of the year. They pass the time in a torpid state, in almost a lifeless condition, requiring no food and but little air. Such a winter sleep, in which animation is suspended, is met with in a number of different animals, and is spoken of as hibernation. In early spring they awake, and

FIG. 1.—The common frog.—From Borradaile.

during February and March are always to be found near water for the purposes of reproduction. The females lay a large number of eggs which are fertilised by the male, and adhere together in jelly-like masses, the spawn, and are common enough in our ponds and ditches. When laid, the eggs are left absolutely alone, and the young frog or tadpole has to fend for itself During the summer frogs often wander quite considerable distances from water in search of food, but always return again in the succeeding spring.

The general features of shape and size, the number and arrangement of limbs and openings, etc., that can be made out without resorting to dissection or opening the animal up are spoken

of as the external characters. You will readily observe that the frog as a whole is divisible into head, trunk and limbs. The head, unlike our own, is not joined to the body by means of a flexible neck, but the two are continuous with one another, a condition that we frequently meet with in water-dwelling animals. For the purposes of description we speak of the back as the dorsal surface, the underneath as the ventral surface, the end that is foremost in moving, *i.e.* the head, as anterior, and the after part of the body as posterior. A little closer observation will show that the skin is quite smooth, and has no structures resembling scales, feathers, hairs or nails upon it. Such structures, when present, as in many animals, we term collectively the **exoskeleton.**

Turning first to the head, we find it possesses a bluntly rounded snout, and that the mouth is a long slit running the greater part of the way round its edge. Two small openings, the nostrils or **external nares,** are situated on the top of the front end of the snout. If the living animal be watched carefully it will be noted that the neck is constantly falling and rising, and at the same time a little flap or valve just inside the external nares is opening and shutting. These movements are concerned with breathing or respiration, and the air is not drawn into the lungs by expanding the chest, as in ourselves, but pumped in by the action of the throat. A short distance behind the external nares are situated the large protruding eyes, whose prominence in some degree compensates for the absence of a neck by allowing a wide field of vision. In each we can make out, as in ourselves, an eyeball, in the middle of which is a circular black space, the **pupil,** through which the light enters, surrounded by a wide coloured band, the **iris.** The upper eye lid is fairly well marked and slightly movable, but the lower one is represented by a very transparent skin, the **nictitating membrane,** which can be drawn right up over the eye. An external ear or **pinna,** such as our own. is absent, but just behind the eye and above and behind the mouth is a circular patch of black, thin, lightly stretched skin. This is the ear drum or **tympanic membrane.**

The trunk is not marked by any striking characters, save that in the sitting position a hump appears in the middle of the back ; the meaning of this will be made clear when the internal structure is examined. It ends bluntly without any tail. At the posterior end of the body, between the hind legs and slightly on the dorsal side, is an opening, the **cloaca,** through which the waste matters and reproductive products are expelled from the body. Attached to the trunk are the limbs or appendages, consisting of a pair of fore limbs or arms, and a pair of hind limbs or legs. The arm is composed, as in ourselves, of an upper arm or **brachium,** a fore-arm or **ante-**

brachium, a small indistinct wrist or **carpus,** and a hand or **manus.** Unlike our own the hand has only four fingers or **digits,** a thumb or **pollex** being absent. The leg similarly is composed of a thigh or **femur,** a shank or **crus,** a very long ankle or **tarsus,** and a foot or **pes.** The foot appears to have six digits, five large and one small, but we shall see later that the small inner one, the calcar, is not a true toe, and the first big one is the great toe or **hallux.** The five large toes are united by a thin fold of the skin, the so-called web, and in this way a large surface for swimming is obtained. The form of the animal is maintained by a number of hard structures or bones, that are felt when handling it, and which together constitute the internal skeleton or endoskeleton, to distinguish it from the exoskeleton.

Among the amphibia in general it is difficult to tell the male from the female externally, but this may be done quite easily in the frog by an examination of the hand. The under side of the inner digit in the male possesses a brownish-black swelling, somewhat like the ball of our limb, but still more marked, while the same digit of the female is not swollen. This enlargement in the male varies at different times of the year, and is particularly well developed during the breeding season. Further, at the same period the male when croaking exhibits two bladder-like swellings, the **vocal sacs,** under its throat, these serve as resonating chambers to increase the volume of sound.

General Internal Structure.

Having considered the external characters, out next duty is to examine the internal structure. If the mouth be opened widely and the joint between the jaws snipped through with the scissors a number of structures can be made out. The roof of the mouth, or **buccal cavity,** is surrounded by the upper jaw, which is immovably fixed to the skull, as in ourselves, and contains a large number of small pointed teeth, the **maxillary teeth.** The roof itself is formed by the base of the skull and the **orbits** or cavities in which the eyes are lodged, and is covered by a very soft moist skin, the mucous membrane. Two very prominent swellings caused by the eyes are readily seen. Just in front of these, nearer the middle line, are two small groups of teeth, the **vomerine teeth,** and in front of these again two small openings, the **internal nostrils** or **nares.** These communicate with the internal nares, as may be seen by inserting a bristle into the latter, by means of a short tube, the **narial passage.** This channel is dilated to form a large narial chamber containing the **olfactory organ,** by means of which the frog is able to smell. Behind and outside the eye swellings at the back of the upper jaw are two

small holes, the openings of the **Eustachian tubes,** and if a seeker be pushed into them it will be found to come to the outside of the head at the tympanic membrane.

The floor of the buccal cavity is bounded by the lower jaw, which contains no teeth, and is covered by the same soft mucous membrane. This jaw is jointed or articulated to the upper jaw in such a way that it is free to move in a vertical direction. The floor itself is soft but supported by a flat plate of gristle or **cartilage,** the **hyoid plate.** Most of its space is occupied by the comparatively large fleshy tongue. This, unlike our own, is bifid at the end, and is attached in front and free at the back, so that it is able to be projected a good distance from the mouth. Behind the tongue is a median slit, the **glottis,** situated on a small oval elevation, the **larynx,** through which the air gains access to the lungs. Right at the back, where floor and roof come together, the cavity narrows somewhat, and is termed the **pharynx.** It communicates with a wide slit, the opening of the œsophagus, which leads to the stomach. If the frog is a male, two small openings lying slightly in front and to the side of the larynx will be seen. These lead into the collapsed vocal sacs, which can be inflated while the animal is croaking, and are particularly marked during the breeding season.

If the frog be pinned out on its back under water the skin can be slit up from the posterior end to the front of the snout, and also a little way along the base of each limb. In doing this it will be noticed that the skin is not attached to the underlying parts, save by one or two bands of thin white substance, the **connective tissue septa.** These divide up the fairly extensive cavity into a number of smaller cavities which, since they are filled with a watery fluid, **lymph,** and are situated under the skin, are termed the **sub-cutaneous lymph sinuses.** A large blood-vessel, the **musculo-cutaneous vein,** will be seen running in the skin in the region of the arm.

Beneath the skin will be seen the flesh or muscles forming the outer wall of the body, arranged in sheets and covered by a very thin layer of semi-transparent substance, the fascia. Passing across the underneath side of the head from jaw to jaw is a broad muscle, the **Mylo-hyoideus.** Posterior to this is a fan-shaped muscle composed of five parts on each side running together at the base of the arm ; this is the **pectoralis muscle.** In the posterior half of the body in the middle line is a thin clear line of connective tissue, the **linea alba,** through which a blood-vessel, the **anterior abdominal vein,** shows clearly. On each side of this line up to the pectoralis the muscles are arranged in a series of small rectangles, the **recti abdominis.** Between the middle parts of the pectoralis muscles and the linea alba is a small plate of cartilage, the **sternum** or heart bone,

underneath which lies the heart. The two hindermost portions of the pectoralis muscle appear to form the body wall, but it will be seen, if they are carefully removed with the scissors, that the true body wall is beneath. If a small portion of the body wall be removed, exposing the internal or body cavity, placed on a glass slide and examined with a lens against the light, it will be seen to consist of two layers of muscles. The outer of these is composed of a thin layer of fibres, the **obliquus externus,** the grain of which runs obliquely upwards and outwards. The external oblique has underneath it an **obliquus internus,** whose grain runs outwards and downwards, and so the two together form the wall of the body.

An incision may now be made in the body wall on one side close to the linea alba from the hinder end forwards. In the region of the middle division of the pectoralis muscle a bone will be encountered. This must be cut through with a strong pair of scissors, care being taken not to go too deeply and damage the underlying structures. A short distance in front of this is another bone that may be cut through in the same way. These two bones form part of a bony framework, the **pectoral girdle,** that supports the fore-limb. A more lateral cut may now be made, great care being taken not to injure any of the large blood-vessels connected with the arm, and so a piece of the ventral body wall will be removed. A similar operation can be performed on the opposite side, thus leaving only a narrow strip of tissue in the middle line. On turning aside this strip in the region of the front end of the linea alba you will see that the anterior abdominal vein leaves it and goes down into the organs of the body. By cutting across the strip just in front of this point the anterior part of it may be removed.*

By thus removing strips of the body wall a large hollow, the body cavity, **cœlom** or **pleuro-peritoneal** cavity, will have been opened up. In it are situated the various internal organs or, as they are comprehensively termed, the **viscera.** In ourselves it is completely divided into two cavities, a pleural and peritoneal, by a transverse sheet of muscles, the diaphragm. The purple-coloured heart will be seen situated close to the sternum in a fairly tight fitting membranous bag, the **pericardium.** Within this bag is a hollow, the **pericardial cavity,** actually a part of the general cœlom that has been cut off. The heart is composed of three separate chambers, a thick-walled posterior pointed chamber, the **ventricle,** and two more anterior thin-walled **auricles.** From the top right-hand side of the ventricle a

* To obtain more freedom in the examination of the various structures, the linea alba with its accompanying vein and small strip of body wall may be tied, *i.e.* ligatured, in two places fairly close together and then cut between. By this means loss of blood is prevented.

stout tube runs forwards between the auricles and then divides up into two trunks, passing right and left. This is the **truncus arteriosus,** and from it spring the arteries or blood-vessels that carry the blood from the heart all over the body. If the heart be turned to one side a triangular very thin-walled sac, the **sinus venosus,** will be seen. Into this open large blood-vessels, the veins, bringing the blood back from the whole of the various parts of the body. A network of blood-vessels will be seen ramifying all over the viscera, and they are termed arteries or veins, according to whether they convey blood away from or towards the heart.

Just behind the heart are two large reddish-brown masses, one on each side. These are the two parts or lobes of the liver, and are joined together in the middle line at the front. Between them will be seen a small thin-walled sac, the **gall-bladder,** usually filled with a dark green liquid, the **gall** or **bile,** which is made by the liver and utilised in digestion. On the dorsal side of the liver and heart will be seen two bright pink sacs with honeycombed walls ; these are the lungs. By inserting a blowpipe into the glottis they can quite easily be inflated and rendered conspicuous.

A large whitish tube will be seen on the left behind the liver. This is the stomach, and if traced forward dorsal to the liver it will be found to merge into a slightly narrower tube, the gullet or **œsophagus,** which in its turn opens into the pharynx. The line of demarcation between the stomach and œsophagus is not nearly so sharp in *Rana* as it is in the rabbit or ourselves. The posterior end of the stomach is marked off by a slight constriction, the **pylorus,** from a very long narrow tube, the small intestine, the first part of which, lying more or less parallel with the stomach, is called the **duodenum,** and the remainder the **ileum.** This pursues a twisted course, and finally expands to form a wide tube, the large intestine or **rectum,** which communicates with the exterior through the cloaca. Thus we find that the food is passed from the mouth into a tube, the **enteric** or **alimentary canal,** which has no openings save the mouth and cloaca. In order that the food may be distributed to the various organs it is necessary for it to pass through the wall of this canal. This is accomplished by its being made soluble or digested.

A small yellow elongated mass is situated between the duodenum and the stomach, this is the **pancreas,** and it also is concerned with digestion.

Near the front end of the rectum is the **spleen,** a globular structure about the size of a small pea and dark red in colour.

The **urinary bladder** is a fairly large bilobed sac with very thin walls, and is to be found opening into the ventral wall of the cloaca and lying in the posterior part of the body cavity.

When we push aside the alimentary canal still other organs are brought into view, these are the reproductive organs, which, as they differ in the two sexes, need separate description. In the male a

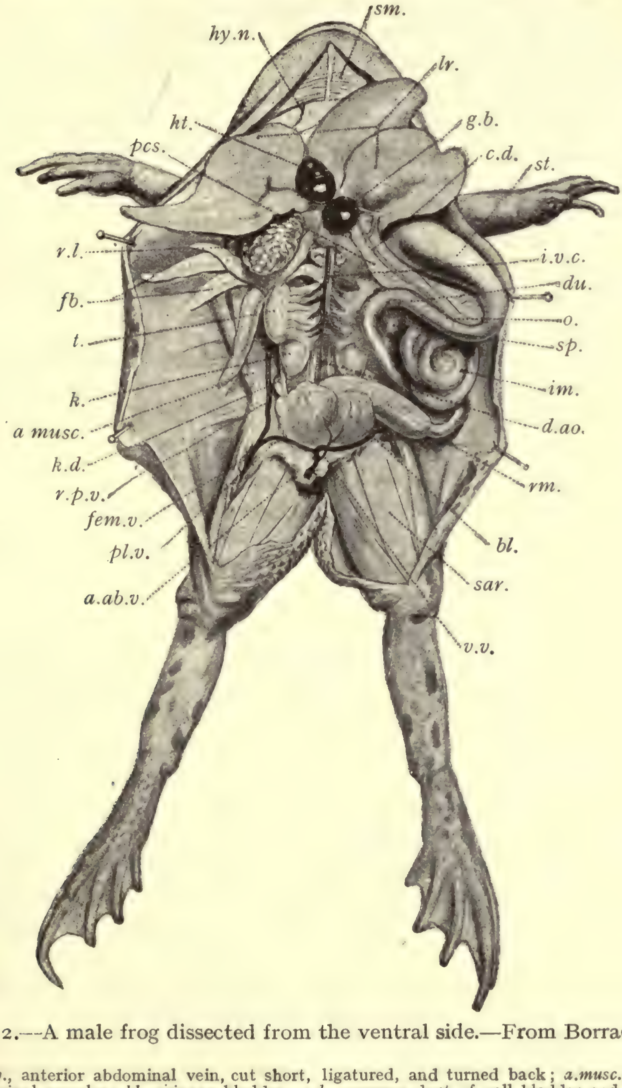


FIG. 2.—A male frog dissected from the ventral side.—From Borradaile.

a.ab.v., anterior abdominal vein, cut short, ligatured, and turned back; *a.musc.*, cut edge of abdominal muscles; *bl.*, urinary bladder; *c.d.*, common duct of gall bladder and pancreas; *d.ao.*, dorsal aorta; *du.*, duodenum; *f.b.*, fat body; *fem.v.*, femoral vein; *g.b.*, gall-bladder; *ht.*, heart; *hy.n.*, hypoglossal nerve; *im.*, ileum; *i.v.c.*, inferior vena cava; *k.*, kidney; *k.d.*, kidney duct with vesicula seminalis; *lr.*, liver; *o.*, point at which *c.d.* enters the duodenum; *pcs.*, pancreas; *pl.v.*, pelvic vein; *r.l.*, right lung; *rm.*, rectum; *r.p.v.*, renal portal vein; *sar.*, sartorius muscle; *sm.*, mylohyoid muscle; *sp.*, spleen; *st.*, stomach; *t.*, testis; *v.v.*, vesical vein.

whitish ovoid body, the **testis,** will be seen on each side. It is covered by a thin skin in which are a number of black pigment cells. A bright yellow finger-shaped structure, the **fat body,** is attached to the front end of each testis.

The primary reproductive organs in the female consist of the **ovaries,** which vary greatly at different times of the year. In the early spring, before the egg laying has taken place, they are very large indeed, and contain a large number of spheres, each composed of black and white halves. These are the **ova** or eggs. After the egg-laying period the ovaries are much smaller, but still of fair size, and are long lobed structures of a greyish colour. A long white coiled tube will be found dorso-laterally to the ovary, extending from the anterior to the posterior end of the body cavity. The **oviduct,** as this tube is named, conveys the eggs to the exterior, and is much larger during the breeding season.

Dorsal to the reproductive organs, and attached fairly closely to the back of the cœlom, are two irregularly oval bodies of a red colour, the kidneys. These are concerned with the elimination of the fluid waste material from the body. From the outer posterior end of each a white tube, the **ureter,** passes backwards to open into the dorsal wall of the cloaca, and this conveys the waste to the exterior. In the male this tube swells out to form a sac, the **vesicula seminalis,** in which the male reproductive elements are stored until required.

The whole of the pleuro-peritoneal cavity is lined by a thin glistening membrane, the **peritoneum,** more or less well supplied with pigment cells. In the mid-dorsal line the membrane on each side passes ventrally and forms a series of folds, the **mesenteries,** each composed of two layers, which hold the various viscera in their places. The layer on the body wall is termed the parietal, and that around the various organs the visceral layer of the peritoneum. Where the two sheets of parietal peritoneum are reflected ventrally to form the mesentery a space is left, the **sub-vertebral lymph sinus.** In this are situated the main artery of the body, the **dorsal aorta,** and a large vein that has its origin between the kidneys, the **post-caval vein.**

On the dorsal side of this sinus in the middle line will be found a jointed bony rod, the backbone or **vertebral column.**

If the frog now be turned on its back and the skin removed, the vertebral column will be seen in the middle line almost completely hidden by muscles. These can be scraped off and the dorsal part of the backbone carefully snipped away with a strong pair of scissors. It will be found that the column possesses a distinct cavity, the **neural canal,** in which is situated a soft rod-like structure,

the **spinal cord.** This is really a tube, but its walls are very thick and the bore very small. If the neural canal be followed backwards it will be found that the spinal cord is reduced to a mere thread before it reaches the level of the hump in the back where the backbone ends. The reduced part passes back in the neural canal accompanied by other similar threads, which also come off from the cord. Sooner or later these pass outwards through the vertebral column to form the nerves. At the anterior end the spinal cord is continued into the head, where it lies in a bony case, the skull. Here, however, it no longer remains simple, but swells out in various parts to form a complex structure, the brain, which we shall have to consider in detail later on. The whole of this soft structure, the brain and spinal cord, is known as the central nervous system, and it is the great controlling and co-ordinating organ of the body. It is connected by nerves with the eyes, ears, nose, etc., whence it receives messages from the outside world, and it is also connected with the various muscles, and so is able to regulate the activities of the animal as a whole.

The frog will serve to illustrate the general plan of structure common to those animals with backbones, *i.e.* **Vertebrate animals.** An elongated cavity, situated partly in the skull and partly in the vertebral column, extends along the head and trunk in the mid-dorsal line, and contains the central nervous system. The nervous system itself is hollow. The **central canal,** as the cavity is called, in the spinal cord enlarges to form a series of spaces or **ventricles** in the brain. On the ventral side, in the trunk only, is another much larger cavity, the pleuro-peritoneal cavity, completely separated from the neural cavity by parts of the backbone and also by the dorsal muscles. A small portion of this is separated off to form the pericardium, which is situated below the gut. A long coiled tube, the alimentary canal, in which a number of different parts are distinguishable, runs through the remaining portion of this cavity, in which are situated the various structures which we term the viscera.

Before leaving the frog its blood should be examined under the microscope. This may be done by putting a drop of it on a clean slide and adding to it a drop of physiological salt solution (*i.e.* ·5 gram of salt dissolved in 100 c.c. of distilled water) to prevent it clotting, and then covering it carefully with a clean cover-slip. It will be found to consist of a fluid or **plasma,** in which float an enormous number of small solid bodies or **corpuscles.** Closer examination will show that these are not all alike, but are of two different sorts. Some of them are oval, constant in form,

and flattened with a bulged central portion ; these are a pale yellowish-red colour, and are called the red corpuscles. The others are less numerous, smaller and colourless. They also differ from the red in that they are not of a definite shape, and if watched carefully will be found to change their shape slightly. They are termed the white corpuscles or **leucocytes.** If a drop of weak acetic acid and some dye, such as methyl-blue or methyl-green, be added to the slide,* an alteration will be seen in both sorts of corpuscles. They both become faintly tinged with the dye, but within them will appear a definite circumscribed part that becomes much more deeply stained. This is the **nucleus,** and all the corpuscles will contain one such body, while certain of the leucocytes may contain more than one.

As we have learned already, living matter is composed of a substance called protoplasm, and now we have seen that in the blood the protoplasm is in the form of small pieces, the corpuscles. Within the corpuscle itself, however, we find that at least two parts are to be distinguished ; a central more dense portion that stains deeply with certain dyes, and, secondly, a surrounding zone, less dense, that stains more lightly. Such a small living mass we designate a cell, and it may be defined as a mass of protoplasm, usually minute, consisting of a central dense deeply-staining nucleus surrounded by a clearer, more lightly staining material, usually termed the **cytoplasm.** The corpuscles are very simple types of cells, and do not exhibit the modifications that we find in the cells which with their products constitute the entire body.

This preliminary investigation of the frog has served to enlarge our conception of a complex animal. We have seen that it is capable of swimming, jumping, and performing a number of voluntary actions that represent a certain amount of work, and need the expenditure of a corresponding amount of energy. Moreover, a very casual examination of the living frog is sufficient to show that the movements of the various parts of the body are not spasmodic, but are co-ordinated in such a way as to produce a definite result. The frog, like all other animals, increases in size, and by means of eggs is able to produce a number of animals, tadpoles, which, after undergoing a series of changes, become similar to their parents. The energy for these various activities is obtained in a potential form from the food, which is first digested and then **assimilated,** or made part of the body of the animal. The energy thus stored is released by slow combustion or **oxidation,** and the

* This process will be hastened if the acetic acid and dye be placed on one side of the cover-slip and the excess of fluid drawn off from the opposite side by means of a piece of blotting-paper, thus causing the two fluids to be drawn under the cover-slip much more rapidly.

oxygen necessary for this process is obtained from the atmosphere by respiration. The oxidation of the various substances results in the production of waste materials, which must be removed from the body or **excreted.** For the carrying on of these processes we find a collecting and distributing agent in the blood, which carries oxygen and food to the places where they are wanted, and also collects up the waste matter so that it can be eliminated by the kidneys and lungs.

In order to perform all the various operations in as efficient a manner as possible, we find that the body is divided up into a large number of separate parts, each specially modified to perform one or two functions; such parts are termed **organs.** Thus the ovaries and testes are reproductive organs, the pancreas and liver digestive organs, and so on. The maintenance of life depends on the correlation of the activities of the various organs, and when an important one of them is put out of action by disease the other vital phenomena of the animal are brought to a standstill, or, as we say, the animal dies. As a rule an organ is not homogeneous throughout, but is composed of various kinds of living material; each separate kind is spoken of as a **tissue.** Again, a number of organs are often linked together, and their functions are contributory to one main end. A group of such organs constitutes a **system.** The alimentary canal with its various parts, the liver and pancreas, form the digestive system for example.

We can thus recognise in the higher animals nine such systems, as follows: (1) the skeletal, (2) the muscular, (3) the integumentary, (4) the alimentary or digestive, (5) the respiratory, (6) the circulatory, (7) the excretory, (8) the reproductive, and (9) the nervous and sensory. In addition to these there are a number of more or less isolated organs collectively termed the ductless glands, whose functions in some cases are but imperfectly understood, and they may conveniently be dealt with together, although they do not constitute a system. We shall now pass on to consider the various systems in *Rana* from the point of view of their structure, both gross and minute, and their physiology.

Skeletal System.

Certain portions of the hard framework, or skeleton, within the body have already been noticed, and it is now necessary to make a more detailed study of its constituent parts. This may be done on prepared skeletons, or, preferably, on one you have made for yourself.*

* A skeleton may easily be prepared by removing as much as possible of the flesh from a frog and then leaving it to go bad or macerate in water. The muscles can then be picked off or removed with a stiff brush. It may be done more quickly, but not so well, by dipping the frog repeatedly into hot water.

The skeleton of the frog consists of two different tissues: a softer, more elastic one, cartilage; and a harder, firmer one, bone. In the tadpole, and even in the young frog, the entire skeleton is formed of cartilage, but as it grows up, although some cartilage persists, the greater part of it is changed. It is replaced by bone, and, in addition, other bones are formed where no cartilages existed previously. These latter are formed by bone tissue being laid down in a membrane, and hence are termed **membrane bones,** to distinguish them from **cartilage bones,** which were preceded by cartilage. This is an important distinction that must be borne in mind when considering the vertebrate skeleton.

The skeleton forms a framework, giving support, rigidity and shape to the whole body. It serves in the main for the attachment of muscles by providing a series of solid structures, which at the same time act as levers and form joints. Although principally concerned with muscular activity, indeed, mainly with locomotion, the skeleton also serves as a protection for the underlying organs in some parts, *e.g.* the sternum protects the heart, and the neural canal and skull protect the spinal cord and the brain.

Like the whole animal the skeleton may be divided into an axial portion, consisting of the vertebral column and the skull, and an appendicular portion, composed of the limbs and the girdles, by means of which they are attached to the body.

Vertebral Column.

The backbone consists of nine short separate parts or **vertebræ,** and a much longer posterior one, the **urostyle.** All the vertebræ, except the first one and the last two, are more or less similar, and any one can be taken as typical. A single vertebra forms an entire bony ring surrounding the neural canal, with a thickened ventral part, the **centrum,** upon which is supported the hoop-shaped **neural arch.** The front end of the centrum is concave and the hinder end convex, a condition which we describe as **pro-cœlus.** The two adjacent ends of succeeding vertebræ fit into one another, and so form a shallow ball and socket joint. To ensure ease of motion they are capped with smooth **articular cartilage,** and between them is a fluid-filled space, the **synovial cavity.** This is surrounded at its periphery by a tough tissue, the **intervertebral capsular ligament.** In the preparation of the skeleton both cavity and ligament are destroyed.

The neural arch on each side is composed of a vertical **pedicle** and a more expanded horizontal **lamina,** forming the roof of the neural canal. In the mid-dorsal line it bears a short backwardly-

directed process, the **neural spine,** serving for the attachment of muscles. A flattened rod of bone, the **transverse process,** passes

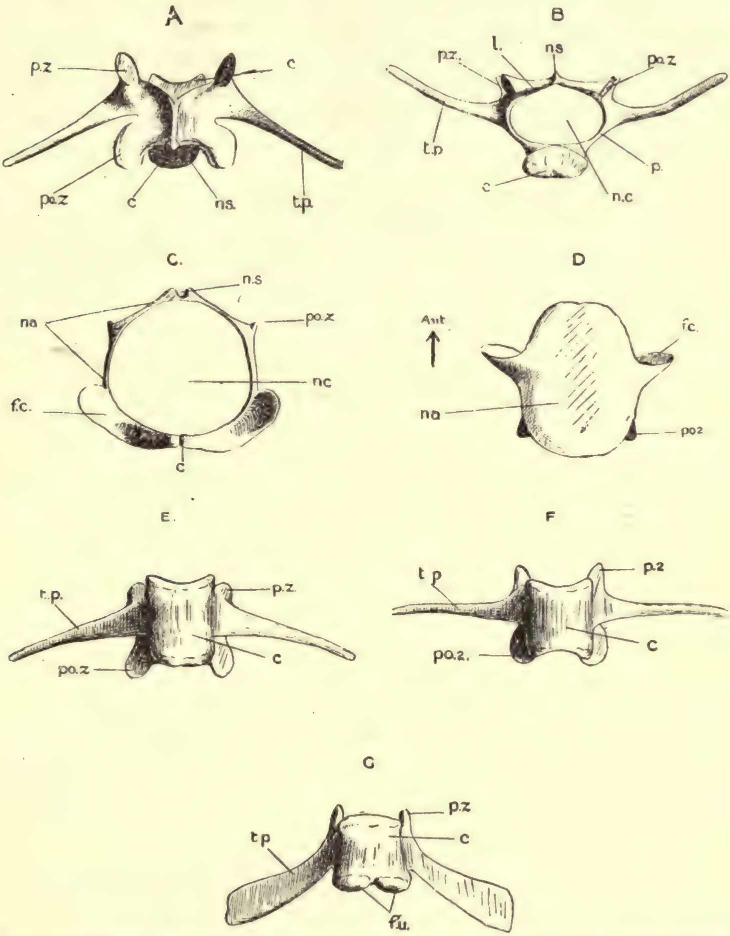


FIG. 3.—Vertebræ *Rana*. A, 5th vertebra dorsal aspect; B, 5th vertebra posterior aspect; C, Atlas anterior aspect; D, Atlas posterior aspect; E, F, G, 7th, 8th and 9th vertebræ ventral aspect.

c., centrum; *f.c.*, facet for articulation with exoccipital bone; *f.u.*, facet for articulation with urostyle; *l.*, lamina; *n.a.*, neural arch; *n.c.*, neural canal; *n.s.*, neural spine; *p.z.*, pre-zygapophysis; *po.z.*, post-zygapophysis; *t.p.*, transverse process.

outwards from the side of the pedicle near its base, and is tipped with cartilage in the second, third and fourth vertebræ.

A pair of processes, the **zygapophyses,** is given off from each end

from the junctions of the pedicles and laminæ. The front or **pre-zygapophyses** have smooth cartilage-covered surfaces, the articular **facets,** facing upwards and a little inwards, while the **post-zygapophyses** have similar facets directed downwards and outwards. Thus, in addition to the intercentral joint or articulation, a pair of zygapophyseal articulations is present between successive vertebræ. It is characteristic of the vertebrates in general that when zygapophyses are present articulating surfaces of the anterior face upwards or inwards, or both, and the posterior downwards or outwards, or both.

The first vertebra, or **atlas,** differs markedly from the rest. The centrum and neural spine are reduced, and the transverse processes and pre-zygapophyses are entirely absent. Its anterior end is provided with two concavities, by means of which it articulates with the skull. The third vertebra has very well-developed transverse processes, serving for the attachment of muscles connected with the girdle bearing the fore-limbs. The centrum of the eighth vertebra is hollow in front and behind, a condition that we describe as **amphicœlous.** The ninth vertebra is also modified, and since its long somewhat backwardly directed transverse processes articulate with the girdle of the hind limbs, it is called the **sacrum.** The front end of its centrum is convex, the posterior end bears two small knobs and has no zygapophyses.

Apart from the differences in detail, the nine vertebræ form a series of similar structures repeated one behind the other. Structures that are alike, made of the same parts, and developed in the same way, are said to be homologous, and when repeated, as in the vertebral column, are described as serially homologous. When placed side by side, as in the living frog, a gap is left between the pedicle of one vertebra and the next. This is the **intervertebral foramen,** and through it the nerves from the spinal cord pass into the body.

The urostyle is a long unsegmented rod of bone, bearing at its anterior end two facets, which articulate with the knob-like projections from the centrum of the sacrum. A short distance behind these is a pair of small foramina, to allow the last pair of spinal nerves to leave the neural canal. The urostyle is to be regarded as representing a series of fused and reduced vertebræ, and faint indications of segmentation, or even traces of one or two vertebræ, are sometimes to be seen at the anterior end.

The frog is markedly different from ourselves in not possessing any ribs nor any indications of them.

Skull.

The skull of the frog, as of all higher vertebrates, consists of a case for the brain, the **cranium,** with which are connected the sense capsules, the jaws and the hyoid apparatus. The sense capsules comprise three pairs : the **auditory,** lodging the organ of hearingand attached to the hinder end of the cranium ; the **olfactory,** lodging the organ of smell and attached to the anterior end ; and lastly, the **optic capsule** or eye, between the former two. In the frog the optic capsule is not attached to the skull, but the other bones are so arranged that a space, the **orbit,** is left for it. Two jaws are present, the upper, firmly, although indirectly, attached to the cranium, and consequently not capable of independent movement, and the lower, connected with the upper by means of a joint at the hinder end, and free to move in a vertical direction. The hyoid

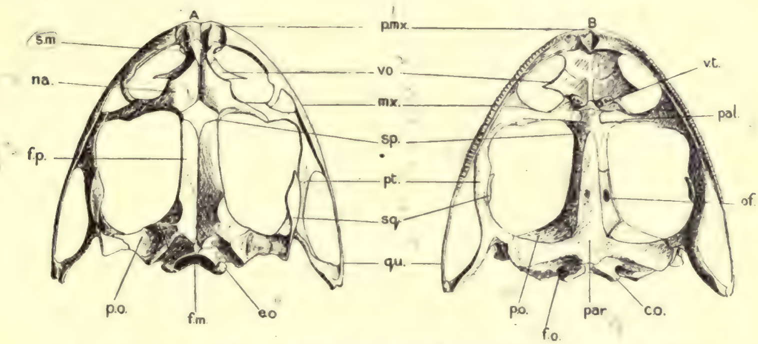


FIG. 4.—The skull of *Rana*. A, Dorsal aspect ; B, Ventral aspect .

e.o., exoccipital ; *f.m.*, foramen magnum ; *f.o.* fenestra ovalis ; *f.p.*, fronto-parietal ; *mx.*, maxilla ; *na.*, nasal ; *o.f.*, optic foramen ; *pal.*, palatine ; *par.*, parietal ; *p.mx.*, pre-maxilla *p.o.*, pro-otic ; *pt.* pterygoid ; *qu.*, quadrato-jugal ; *s.m.*, septo-maxillary ; *sp.* sphenethmoid ; *sq.*, squamosal ; *vo.*, vomer ; *v.t.*, vomerine teeth.

apparatus consists of the flat hyoid plate, situated as already noted, in the floor of the mouth, and its projecting horns.

In the middle of the back of the skull is a large hole, the **foramen magnum,** through which brain and spinal cord are continuous. On each side of this, and forming its entire margin, save for small pieces of cartilage in the mid-dorsal and ventral lines, is a cartilage bone, the **exoccipital,** which is produced backwards into a rounded knob, the occipital condyle. The condyle fits into and articulates with the corresponding concavity on the front of the atlas vertebra. If the skull be placed in its natural position with regard to the atlas, it will be seen that on the dorsal surface a considerable space is left between it and the neural arch of the atlas.

In life this space is covered by a tough skin, the **atlanto-occipital membrane.** The exoccipital not only forms the back of the cranium, but also the back and part of the floor of the auditory capsule, which forms a prominent structure fixed to each side of the hinder end of the cranium. The front wall of the capsule is formed by another cartilage bone, the **pro-otic,** at whose lower inner corner is situated a foramen, through which the fifth, sixth and seventh nerves given off from the brain leave the skull. The lateral wall of the auditory capsule, its roof and floor, are formed of cartilage more or less covered by superposed membrane bones. In the posterior part of the lateral wall is a small opening, the **fenestra ovalis,** leading to the sensory part of the ear. This is closed by a small block of cartilage, the **stapes,** to which is attached a short thin bony rod, the **columella,** and this in its turn is connected with the tympanum.

From the auditory capsule the cranium is continued forward as a cartilaginous tube to the front end of the orbit. Half-way along its side it is perforated by a large circular foramen, through which the second nerve from the brain passes to the eye. The dorsal surface is also incomplete, and is perforated at the front end by a large hole, the **anterior fontanelle,** and at the hinder end by two smaller holes, the **posterior fontanelles.** The fontanelles are completely hidden by the paired overlying membrane bones, the **fronto-parietals,** which spread out slightly at the posterior end and help to cover the inner part of the roof of the auditory capsule. The cartilaginous floor of the cranium is similarly covered by a membrane bone, the unpaired **parasphenoid,** a T-shaped bone, whose arms underly the whole of the bases of the auditory capsules.

The anterior end of the cranium is formed by the girdle bone, or **sphenethmoid.** This is a cartilage bone completely encircling the cranium, and it has a deep hollow at each end. The partition between the two cavities is perforated for the passage of the nerves of smell. It is a bone that is peculiar to the Amphibia. The cavity at the front end is divided into two, a right and a left, by means of the cartilaginous internasal septum, which passes forwards and completely separates the two olfactory cavities from one another.

The front end of the cranium bears the two olfactory capsules, two incomplete cartilaginous structures. Over the dorsal part of the capsule is situated a triangular membrane bone, the **nasal,** and just in front of this is a very small bone, the **septomaxillary.** A triangular membrane bone, the **vomer,** lies beneath the capsule and bears at its hinder inner corner a small group of pointed teeth, the vomerine teeth, while its hinder outer corner is deeply notched to form the boundary of the internal nostril.

The outline of the lower part of the skull is arch-shaped, and

is formed by the two jaws, both of which are first laid down in cartilage. The upper jaw in the adult, however, is covered by three membrane bones. The **quadrato-jugal** is a short bone sheathing the jaw at its hinder end and bearing no teeth. From this the much longer **maxilla** runs forward, and lastly, the front part is completed by a smaller bone, the **pre-maxilla,** which joins its fellow in the middle line and also sends a small dorsal process backwards to form the inner boundary of the external nostril. Both the pre-maxilla and maxilla bear a row of small sharp conical teeth. The upper jaw is immovably fixed to the cranium at the posterior end and again near the anterior end. The hinder connection is made by the **quadrate cartilage,** or, as it is also termed, the **suspensorium.** This is a cartilaginous rod, forked at its inner end, that runs outwards from the side of the auditory capsule and bears at its outer end a hollow, **glenoid cavity,** with which the lower jaw articulates. The dorsal side of the suspensorium is covered by one limb of a large tri-radiate membrane bone, the **squamosal,** of whose other limbs one runs to the pro-otic bone and the other forwards towards the second point of attachment of the upper jaw. A similar triradiate bone, the **pterygoid,** in part underlies the quadrate cartilage. Its three limbs are similarly distributed, and the anterior one reaches and joins with the upper jaw. The anterior attachment of the jaw is also formed by a bar of cartilage, the **palatine cartilage,** passing outwards from the sphenethmoid bone. This is underneath the hinder edge of the nasal bone and encased on the ventral side by a slender membrane bone, the **palatine bone.** Like the pterygoid, the palatine bone in the higher animals is a cartilage bone, but this is not so in *Rana*.

The lower jaw or **mandible** is similarly a cartilaginous arch, **Meckel's cartilage,** almost entirely covered by membrane bones, none of which bears teeth. The posterior covering bone is the short **angulo-splenial,** which possesses a small articular knob, and in front of it is situated the long **dentary.** At the anterior end in young frogs a small piece of cartilage is left, but in older skulls this ossifies to form a small bone, the **mento-meckelian,** and the two halves of the jaw are bound together by a tough ligament.

The hyoid cartilage, or body of the hyoid, situated in the floor of the mouth, is a thin shield-shaped plate, giving off processes at its fore and hind ends. The anterior processes, or **cornua,** are very slight and cartilaginous, and pass first forwards, then backwards and upwards. They are finally attached to the back of the auditory capsules, and the columellæ are formed from small pieces separated off from their anterior ends. The posterior cornua are short somewhat stout rods of cartilage bone, that pass back one on each side of the glottis.

Appendicular Skeleton.

The skeleton of the fore-limb consists of a number of bones, which may be divided up in the same way as the limb itself. Inside the brachium is a single bone, the **humerus,** which serves as a good example of what is known as a long bone, and is divisible into a proximal part, *i.e.* the end near the body called the head, a long middle part the shank, and a distal portion the condyle. Like all the bones of the limbs it is a cartilage bone, and its two ends, termed **epiphyses,** ossify separately from the shank, with which they afterwards fuse. The head of the humerus is rounded and covered with articular cartilage. From its head a strong keel, the **deltoid ridge,** runs along the front side of the shank. The distal end has two prominent lateral **condylar ridges,** between which is a depression, the **trochanter,** in part filled with a knob covered with articular cartilage. The skeleton of the antibrachium consists of a bone, the **radio-ulna,** formed by the union of two separate bones, the radius and ulna, showing distinct signs of its double origin. Its proximal end is hollowed to receive the humerus, and it projects backwards beyond this as the **olecranon process.** At its distal end it articulates with a series of six wrist bones, or **carpalia.** The first row consists of three bones called the **radiale,** the **intermedium,** and the **ulnare.** The first and last are situated at the ends of the radial and ulnar parts of the combined bone, and the intermedium lies between them. The second row also consists of three bones, two small ones and a larger posterior one, representing three smaller ones fused together. Following this comes the skeleton of the manus. The proximal part consists of a row of five small bony rods, the metacarpals. The anterior of these is smaller than the rest, and is all that remains of the first digit, the pollex or thumb. The other metacarpals are followed by a varying number of small rods, the **phalanges.** Two are borne on the first or fore-finger, two on the second, and three each on the third and fourth. When a limb is stretched out the side on which the big toe or thumb is situated

FIG. 5.—Longitudinal section of the femur, showing the compact and cancellous tissues, and the medullary cavity.—From Furneaux.

is termed the anterior or **pre-axial** border of the limb, and the other the posterior or **post-axial** border.

The fore-limb is attached to the body by means of the pectoral girdle, which consists of a bony framework, almost completely encircling the body, but incomplete on the dorsal side. Each half is divided into two portions by the **glenoid cavity,** a hollow depression lined by articular cartilage, into which the head of the humerus fits. The dorsal, **scapular part,** consists of two elements, a fairly stout cartilage bone, the **scapula,** which forms part of the glenoid cavity, and a thinner wider bone, the **supra-scapula,** situated more dorsally. The supra-scapula never completely ossifies, and its dorsal edge is

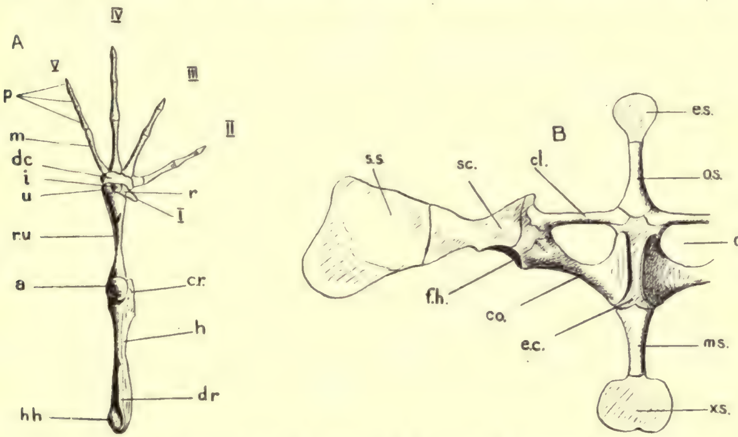


FIG. 6.—A, Left fore-limb *Rana*; B, Left half pectoral girdle *Rana*.

a., articular knob of humerus ; *c.f.*, coracoid foramen ; *cl.*, clavicle ; *co.*, coracoid ; *c.r.*, condylar ridge ; *d.c.*, distal carpalia ; *d.r.*, deltoid ridge ; *ec.*, epicoracoid ; *es.*, episternum ; *f.h.*, facet for articulation with head of humerus ; *h.*, humerus ; *h.h.*, head of humerus ; *m.*, metacarpalia ; *ms.*, mesosternum ; *os.*, omosternum ; *p.*, phalanges ; *r.*, radiale ; *r.u.*, radio-ulna ; *sc.*, scapula ; *s.s.*, supra-scapula ; *u.*, ulnare ; *xs.*, xiphisternum ; *I.*, 1st metacarpal ; *II.–V.*, digits.

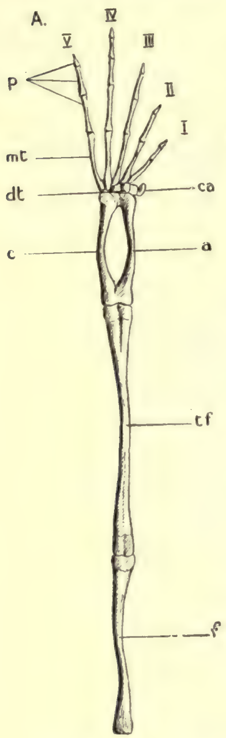
always formed of cartilage. The ventral part of the girdle is known as the **coracoid portion.** From the anterior corner of the glenoid cavity a narrow rod, the **pre-coracoid,** runs inwards toward the middle line, not quite meeting its fellow from the opposite side. Actually only a very narrow strip of this is visible, because a thin bone, the clavicle, is wrapped round it. The **clavicle** is the only membrane bone in the appendicular skeleton, and may or may not be represented in ourselves by the collar bone. The posterior ventral part of the glenoid cavity is formed by the **coracoid** bone, which passes inwards and backwards, leaving a space, the **coracoid foramen,** between it and the clavicle. Its inner end is expanded, but, like the pre-coracoid, does not touch its fellow of the other side. The

inner ends of the coracoid and pre-coracoid are joined by a narrow strip of cartilage, the **epicoracoid,** and the two epicoracoids meet in the mid-ventral line. Passing forward from these, also in the middle line, is a short bony rod, the **omosternum,** and in front of this is a thin circular plate of cartilage, the **episternum.** Behind the epicoracoids is a bony bar, the **sternum** or **mesosternum,** and posterior to this again is a bilobed cartilaginous expansion, the **Xiphisternum.** It has been pointed out previously that in addition to supporting the fore-limbs and giving attachment to their muscles the ventral part of the pectoral girdle forms a protection for the heart. Although single in the adult, the various sternal elements arise from the paired rudiments. It is not yet clear how far they correspond to the breast bones in man, for they arise in connection with the coracoid bones, whereas in man the sternum is developed in relation to the ventral ends of the ribs.

The bones of the hind-limb are very similar to those of the fore-limb and homologous with them. The bone of the thigh is the **femur,** a long slightly curved bone with a well-marked rounded head and the distal end expanded laterally. The leg contains the **tibio-fibula,** and the well-marked groove running along this indicates its origin from two separate bones. In the tarsus are two rows each of two bones. The proximal two are quite long and united together at both ends. The pre-axial bone is termed the **astragalus,** and the slightly larger post-axial one the **calcaneum.** The distal tarsalia are quite small and easily overlooked. Unlike the hand, five complete digits are present in the foot, and there is also a small additional toe. Each digit has a well-developed **metatarsal,** and the number of phalanges is two on the first and second toes, three on the third and fifth, and four on the fourth. The extra toe, or **calcar,** consists of a very short broad metatarsal on the pre-axial side of the **hallux** or big toe, and sometimes also indications of a phalanx. Supporting the calcar is a small bony nodule that may represent a displaced tarsal.

The hind-limb is suspended by the pelvic girdle In its primitive condition this girdle, like the pectoral, forms an incomplete hoop around the posterior part of the body. It has been modified in the frog in accordance with the jumping habits of the animal, and the ventral end has rotated through an angle of nearly 90 degrees, so that instead of passing to the ventral side it is dorsal and almost in a line with the backbone. The conspicuous hump on the back of the frog marks the point of attachment of the pelvic girdle to the backbone. The girdle is similar in shape to the " wish-bone " or merrythought of a bird, and it exhibits on each side a deep cup-shaped hollow, the **acetabulum,** into which the head of the humerus fits

The two long bones articulating with the processes of the sacral vertebræ are the **ilia**. Each possesses a well-marked crest, and unites with its fellow posteriorly in the middle line to form a part of the acetabulum. The remaining part of the wall of this depression is formed by two bones, in front by the small **pubis,** which never completely ossifies, and the larger posterior part by the bony **ischium.** These three bones, ilium, ischium, and pubis, meet the corresponding ones of the opposite side in the middle line in junctions termed **symphyses.**



Before leaving the skeleton it will be well to examine its structure in detail as revealed by the aid of the microscope. Good

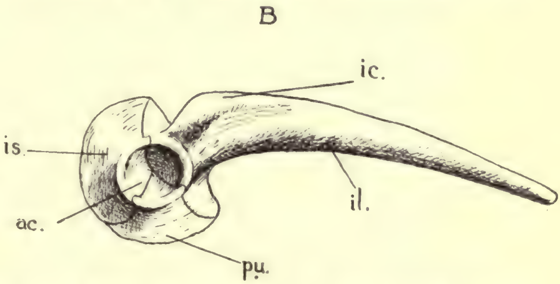


FIG. 7.—A, Left hind limb *Rana* ; B, Pelvic girdle *Rana* viewed from right side.

a., astragalus ; *ac.*, acetabulum ; *c.*, calcaneum ; *ca.*, calcar ; *d.t.*, distal tarsalia ; *f.*, femur; *i.c.*, iliac crest ; *il.*, ilium ; *is.*, ischium ; *mt.*, metatarsal ; *p.*, phalanges ; *pu.*, pubis ; *t.f.*, tibio-fibula ; *I.–V.*, digits.

examples of cartilage may be obtained by taking thin slices of the head of a large bone, or of the epi- or xiphisternum, and examining them in normal salt solution under the microscope. It consists of a large number of slightly granular cells embedded in homogeneous fairly clear substance, the **matrix.** The nuclei of the cells can be readily made out by the addition of a drop or two of weak acetic acid and of methyl green. This treatment also shows that a thin layer of the matrix immediately surrounding the cell, termed the capsule, stains more deeply than the rest. The cells, although sometimes single, are more often to be found in groups of two, three or four, in each case derived from the division of a single cell. From the fact that the matrix in these cases is very clear, the substance is

described as **hyaline cartilage.** The supra-scapular yields another variety of cartilage, namely, **calcified cartilage,** so called because the matrix is more or less impregnated with calcareous granules. These may be removed by immersion for some time in weak hydrochloric acid, and the matrix then appears full of a number of tiny spaces in which the granules were previously lodged.

Young cartilage is easily distinguishable from old, because it possesses much less intercellular matrix, and consequently a relatively larger number of cells. All cartilage on boiling yields a substance called **chondrin,** which sets in a jelly when cold. It is

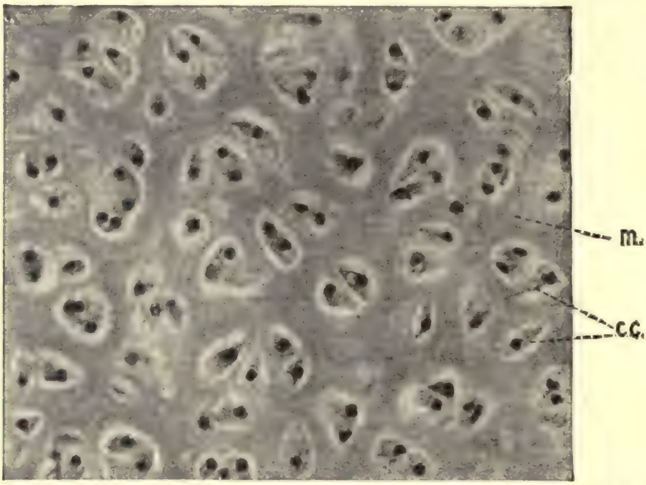


FIG 8.—Section of cartilage, showing cartilage cells (*c.c.*) embedded in the transparent intercellular matrix or ground substance (*m*). × 390.—From a photograph (Dendy).

covered by a tissue containing a rich supply of blood-vessels, known as the perichondrium.

Bone differs markedly from cartilage in many ways, although it agrees with it in being built up of cells surrounded by a large amount of intercellular matrix.. The matrix consists of a tough organic basis, that yields **gelatin** on boiling, densely impregnated with inorganic salts. The intimate way in which organic and inorganic constituents are mixed may be seen by taking two bones and placing one in weak Hydrochloric acid and heating the other in a test tube until it is thoroughly charred. The former will have all the inorganic salts removed, *i.e.* be decalcified, and will be soft and flexible, whereas the latter will have no organic matter left, and will be hard and very brittle. Both, however, will remain

exact models of the original bone. The decalcified one will be about one-third the weight it was originally, and the burnt one about two-thirds. The inorganic salts present in the matrix are mainly Calcium phosphate, but small amounts of Calcium carbonate and fluoride and Magnesium phosphate are also present.

Most of the long bones are hollow, the central cavity in life being filled with a soft red tissue, the marrow. This consists of a plentiful supply of blood-vessels embedded in a fatty substance, in which are special cells, the marrow cells, concerned with the storing of fat and the production of red blood corpuscles. The outer layer of the

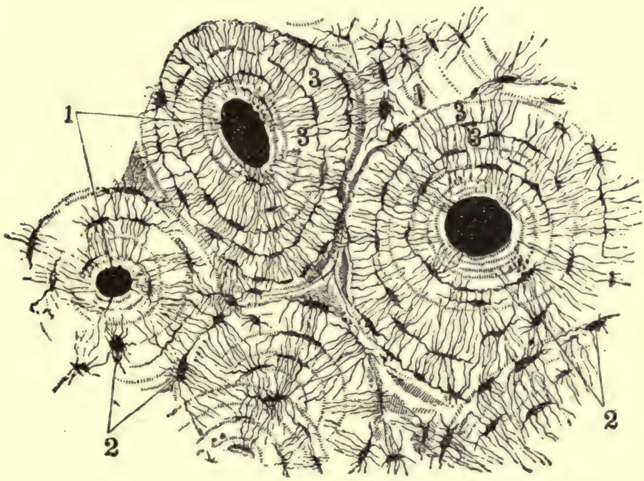


FIG. 9.—Transverse section of the compact tissue of bone. Magnified 150 diameters.—From Quain.

1, Haversian canals ; 2, lacunæ ; 3, laminæ.

bone, *i.e.* the **compact bone,** is much denser and firmer than the inner layer surrounding the marrow cavity, which is termed **cancellous,** but both have the same fundamental structure. The interior of many of the smaller bones, although containing no cavity, is cancellous.

The matrix of bone is quite impermeable to nutriment, and consequently we find an elaborate arrangement to allow of its distribution. Bone, unlike cartilage, is penetrated by a series of blood vessels running in canals called after their discoverer, the **Haversian canals.** In a transverse section these appear as circular spaces, often black when viewed under the microscope, owing to their being filled with air or dirt. Around these the bone is arranged in a series of thin concentric sheets, the **Haversian lamellæ,** marked

off by a similar concentric arrangement of spaces, **lacunæ,** in which the **bone cells** or **corpuscles** are situated. A number of branching canals, the canaliculi, come off from the lacunæ and traverse the lamellæ, thus connecting together the rings of the lacunæ and the Haversian canal. The lacunæ and canaliculi are also black in sections, but in life are filled by cells which give off fine branches, and in this way provide a series of channels through which the food substances brought by the blood may be dispersed throughout the bone. The whole arrangement of canal, lacunæ and canaliculi is known as an **Haversian system.**

In addition to the Haversian, there is always a series of lamellæ on the outside of the bone and parallel with it. These are termed the **peripheral** or **circumferential lamellæ.** In the long bones the marrow cavity is similarly lined by a series of **perimedullary lamellæ.** The small spaces between the three various sets are filled in by yet other lamellæ, the **interstitial.**

The foregoing description of the appearance of bone applies equally to both membrane and cartilage bone, the difference between them being solely whether they are preceded by cartilage or not. It is, however, based on the structure of the bones in the higher vertebrates, such as the rabbit or man, and not strictly applicable to the frog. In this animal we find that the Haversian systems are never fully developed, so that in a transverse section of a long bone we find only a continuous series of concentric lamellæ, the outer of which may be termed peripheral and the inner perimedullary.

The free surface of bone is covered by a formative and nutritive tissue, the **periosteum,** composed of two layers. The outer is fibrous and plentifully supplied with blood-vessels, and the inner composed of a layer of bone-forming cells or **osteoblasts,** left over from those that produced the bone.

The process of bone formation or **ossification** is complex, and only its main features need be noted. In the case of a membrane bone, the place it will take is occupied by connective tissue, whose structure will be dealt with more fully later. Thin strands of the matrix of the future bone are laid down, and the osteoblasts or bone-formers arrange themselves in a more or less regular layer around them. Here they deposit layers of bone, with the result that bony spicules are produced. More strands of matrix are laid down and surrounded by bone in a similar way, and so a network of spicules is produced, at first loose but becoming more and more compact. During this process certain osteoblasts are included in the bone, and form the future bone corpuscles. In cartilage bone a model of the bone is already present and enclosed in perichondrium. Ossification takes place in this surrounding tissue in

a way similar to that already described, and so produces the **perichondral** bone outside the cartilage. **Calcification** or the deposition of lime salts has already occurred to a certain extent in the cartilage. While the perichondral bone is forming, the formative layer sends processes inwards, which first destroy the cartilage by means of special cells, the **osteoclasts,** and then lay down strands of matrix, around which bony spicules are formed. The bone thus formed in the actual position of the cartilage is termed **endochondral.** Ossification continues until peri- and endochondral bone have joined up and the whole of the original cartilage has been replaced. We are now in a position to understand a little more clearly what is meant by the term "epiphysis." In a large number of bones, particularly the long bones, the process of ossification starts from three places, the middle and each end, so that the bone really consists of three pieces, which grow together by an interlocking of the bony spicules. This interlocking is not always complete, so that in a dried skeleton the epiphyses may fall off.

Connective Tissue.

Another tissue may conveniently be considered here, although it cannot strictly be considered as forming part of the skeleton. It helps to bind the various soft parts to one another and to the skeleton, and is therefore called **connective tissue.** In *Rana,* although it is present in small quantities between the fibres of the muscles, we do not find the simplest kind of connective tissue nearly so plentifully as in the rabbit, where it may be obtained readily immediately under the skin. Under the microscope the **sub-cutaneous** or **areolar tissue** appears as a network of interlacing fibres and a number of more or less isolated cells contained in a colourless matrix. The cells, termed **connective tissue corpuscles,** are of at least three different kinds. The **lamellar cells** are flattened, have a large nucleus, and give off a number of processes, which may unite with the similar processes from neighbouring cells. The **granular cells** are more regular in shape with a well-marked nucleus, and owe their name to their granular contents. The granules are coarse and stain deeply with eosin and certain other acid dyes, so that they are often termed eosinophilous. The **vacuolated cells** are frothy in appearance, owing to the number of minute vacuoles present in them.

In addition to these cells, more or less constant constituents, others may be present. A certain number of leucocytes are almost always to be found in the frog pigment cells also.

Two sorts of fibres will be easily distinguished crossing and

intercrossing through the matrix in all directions. **White fibres,** so called from their colour, appear as fairly large bundles of smaller parallel fibres running together and having an undulating course. These do not branch, and fibres from one bundle do not join with those from another. On boiling they yield **gelatin,** and the addition of a drop of acetic acid while they are still fresh causes them to swell up and dissolve. The **yellow elastic fibres** differ from the former in a number of ways. Their course is nearly straight, or only in very shallow curves, and they branch frequently, the branches anastomosing with neighbouring fibres. They are yellow in colour,

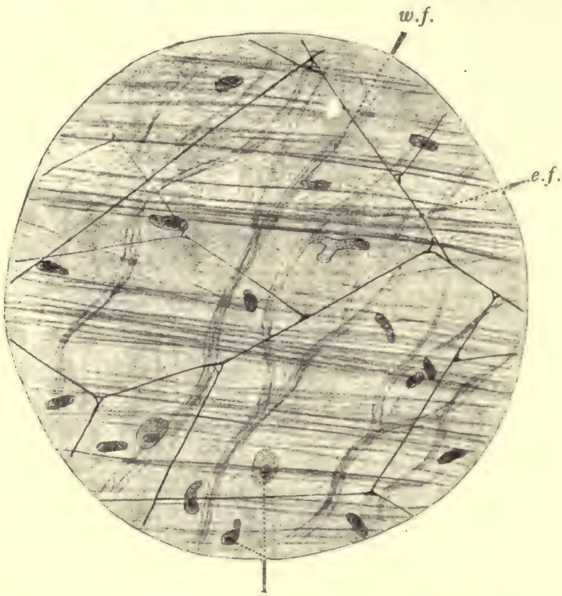


FIG. 10.—Areolar connective tissue of the frog.—From Borradaile.

c., cells; *e.f.*, elastic fibres; *w.f.*, white fibres.

and their cut ends curl up, indicating their elastic nature. Acetic acid has no effect on them, and when boiled they give **elastin** and not gelatin.

Various modifications of this tissue occur to meet different requirements. In tendon and ligament the white fibres run parallel with one another and nearly straight, and they form practically the whole of the structure, the other elements being correspondingly reduced. In the mammals a strong ligament, the **ligamentum nuchæ,** runs along the anterior part of the backbone and is attached to the head, which it helps to hold up. This consists of yellow elastic tissue, in which the elastic fibres form the major part.

Besides the hyaline cartilage already described, two other varieties, white fibro-cartilage and elastic fibro-cartilage, are met with in the mammals. As their names imply, one or other sort of fibre is present in addition to the hyaline matrix. Membrane bone is laid down in connective tissue, and, as has been pointed out, during the formation of cartilage bone the cartilage is destroyed and the bone actually deposited in a sort of connective tissue. Hence it is that some writers regard both cartilage and bone as highly modified forms of connective tissue.

The corpuscles of connective tissue may take up fat, and so the tissue becomes somewhat fatty. This must not be confused with true fat or **adipose tissue.** In this we find numbers of cells, each containing a relatively enormous globule of fat, and the protoplasm is reduced to a very thin enclosing layer, thickened at one point where the nucleus is situated. These fat cells are bound together in groups or lobules by connective tissue. The fat is formed gradually as a number of minute globules within the cell, which ultimately run together and form the large globule.

We have thus seen that the skeleton forms a framework of firm supports of characteristic structure, articulating one with another by means of joints. The soft parts of the body are connected with the skeleton, and the various parts of this with one another by means of connective tissue.

Muscular System and Integument.

It has already been seen that the flesh or muscle is situated beneath the skin and forms the mass of the limbs and the body wall. Muscular tissue is the tissue that is specially modified in order to bring about movements of all kinds. The property of contractility is common to all protoplasm to a certain limited extent, but in muscle it is much more highly developed than elsewhere. Any change that is capable of bringing into activity the whole or any part of an animal, however small, is spoken of as a **stimulus.** Stimuli may come from inside the organism, *i.e.* be internal, or from its surroundings, *i.e.* be external. The stimulus that causes muscle to contract is usually nervous, taking the form of a message from a nerve cell in the brain or elsewhere, although, when a muscle is removed from the body, the same response may be obtained by mechanical, chemical or electrical means, or by the application of heat. When muscle contracts in reply to a stimulus it shortens in the direction of its long axis and increases correspondingly in thickness. The energy necessary for such activity is obtained by the oxidation of the substances of the protoplasm itself, *i.e.* by katabolism.

The muscles in the frog are fibrous in structure and of two kinds. The first are those forming the muscles of the body wall and limbs, and their fibres, grouped in bundles, appear transversely striped when examined under the microscope. They are consequently termed **striate** or, because they can be made to contract at will, **voluntary muscles.** The second kind is found in the walls of the alimentary canal, the bladder and blood-vessels, and does not appear striped. They are called **non-striate muscles,** and, as they are not under the control of the will, **involuntary.** In general we find that striate muscles are directly or indirectly connected with the skeleton, whereas the non-striate are related to the internal organs, and hence the two are sometimes distinguished as skeletal and visceral respectively.

FIG. 11.—Two non-striate muscle cells from wall of intestine showing nuclei and longitudinal striations.

Involuntary muscles consists of a number of long spindle-shaped cells about 1 mm. in length, with pointed ends, that may in rare instances be bifurcated. The cell body is enclosed by a definite membrane, and within it is situated a characteristic elongated nucleus. The cell as a whole is highly refractive, but distinctly granular in the neighbourhood of the nucleus, and may appear very faintly striated in the longitudinal direction, owing to the presence in it of a number of extremely fine fibrils. The cells are situated in layers closely bound together, so that their individual outlines cannot be made out save in preparations from material that has been allowed to stand in certain solutions * and then teased, *i.e.* torn up with fine needles. They lie parallel with one another, and are bound together by a small amount of intercellular substance. Such muscles do not appear to be capable of quick movement in unison, but are adapted for slower ones, such as are required in the blood-vessels and bladder, or the rhythmic contractions, **peristalsis,** that pass along the alimentary canal during digestion.

Many of the skeletal muscles, such as the **biceps,** the large muscle that draws up the fore-arm, and the **gastrocnemius,** that forms the calf of the leg, have a very characteristic shape. They are spindle-shaped, tapering off at each end and swelling out in the middle to form the belly. The ends are continued on as the connective tissue ligaments, and these in turn are joined to the skeleton. When

* Such a process is termed maceration. The fluid may be very weak spirit or a weak solution of Potassium bichromate.

the muscle contracts one of the bones remains more or less still and the other is drawn towards it. The tendon attached to the relatively fixed point is termed the origin, and that attached to the movable bone the insertion. Usually a muscle has but one origin and one insertion, but it may have two, as, for example, in the biceps, which receives its name from the fact that it has a double origin. The tendons are not always united to bone. The distal tendon of the gastrocnemius is called the **tendo Achillis,** and in the frog it passes over the place occupied by the heel in ourselves, and is inserted into a sheet of connective tissue spread out over the sole of the foot. A connective tissue sheet serving for the attachment of muscle or tendon is termed an **aponeurosis,** and the particular one just described, from its position, is known as the **aponeurosis plantaris.**

The entire muscle is enclosed in a connective tissue sheath, the

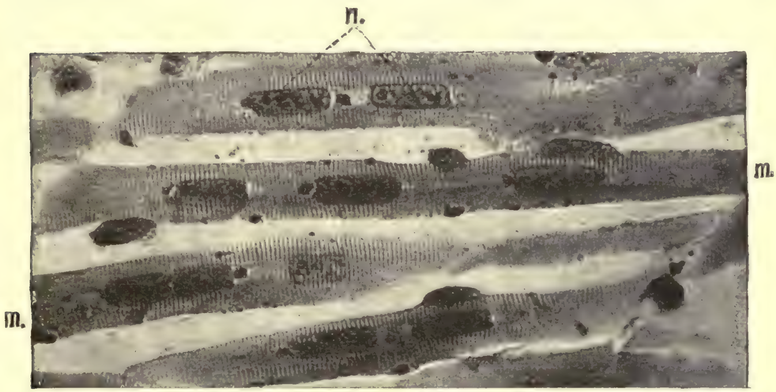


FIG. 12.—Striped muscle fibres (*m.*) from the tail of a larval axolotl, showing their nuclei (*n.*). × 560.—From a photograph (Dendy).

perimysium, and within this are to be found a number of bundles of fibres or **fasciculi,** each enclosed by a sheath, the **endomysium,** continuous with the external one. The individual fibres composing the fasciculi have quite a fair diameter, as much as 1 mm., and may in some cases reach a length of 120 mm. (nearly five inches). They are circular or polygonal in cross-section, and as a rule unbranched, although branched fibres are present in the tongue muscles. Each fibre is enclosed by a very thin sheath, the **sarcolemma,** immediately beneath which are numerous nuclei irregularly distributed. The interior is filled by a semi-fluid substance, the **sarcoplasm,** consisting of a large number of small fibrils parallel with one another, and a certain amount of other material. These fine fibrils are the **fibrillæ** or **sarcostyles,** and give the whole fibre

a faint longitudinal striation. A sarcostyle appears striated from the presence in it of two substances, one of which is clearer and singly refracting, **isotropic,** and hence appears light, and the other is dense, doubly refractive, *i.e.* **anistropic,** and so appears dark. The whole fibre appears striped, because the dark and light bands of the various fibrillæ coincide. When examined under a still higher power of the microscope the light band is seen to be divided into two by a very thin dark line, usually taken to be partly membranous, and so called **Krause's membrane.** Between one membrane of Krause and the next, therefore, is included half a light band on each side of a complete dark band, and this constitutes a unit of striate muscle, a **sarcomere,** and a row of such end to end forms a sarcostyle. The dark band is similarly divided into two parts by a narrow white line, **Henson's line.** The fibrillæ may or may not be uniformly distributed throughout the fibre, and often in a cross-section we find them grouped together in polygonal areas, the **areas of cohesion** or muscle columns. Striate muscle is not composed of simple uninucleate cells, but, as has been pointed out, beneath the sarcolemma are numbers of nuclei. It is found that in development all the structures in one fibre are formed from and by a long multinucleate piece of protoplasm, which arises by the union of many cells. Such a cell fusion is termed a **syncytium.**

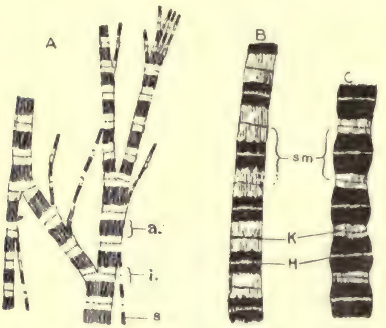


FIG. 13.—Striate muscle. A, Muscle fibre partly teased; B, part of single fibrilla or sarcostyle in resting condition, highly magnified; C, part of single fibrilla in state of contraction, highly magnified.

a., amisotropic element; *H.*, Henson's line; *i.*, isotropic element; *K.*, Krause's membrane; *s.*, sarcostyle; *sm.*, sarcomere.

This striped muscle is well adapted for strong quick movements, such as are required in locomotion, and the various constituent fibres contract in unison, a wave of contraction passing along them from the origin and affecting the sarcomeres successively. The muscle is under the control of the will, and the nerve supplying it branches on entering its substance. The small terminal branches are joined to the muscle fibres by characteristic structures known as **end plates,** and so all the fibres can be called into activity simultaneously. As a result of a change in the disposition of its constituent substances each sarcomere shortens in length and increases in diameter. It appears as if the material of the light bands passes into that of the

dark, so causing them to expand laterally. These changes are also accompanied by chemical and electrical ones, and by the production of heat.

Yet another kind of muscular tissue is met with in vertebrate animals, but it is confined to the heart, and hence termed cardiac. It is involuntary and yet striped, and so constitutes a variety of its own. It is composed of flat short cells placed end to end, with short branches connecting them with neighbouring cells. No sarcolemma is present, and each cell possesses a single fairly large nucleus situated near its centre. It exhibits both longitudinal and transverse stripes, though the latter are not so well marked as in voluntary muscle.

Integument.

The integument in the frog is very simple, and consists only of the skin, in which no hair, nails, or any exoskeletal structures are developed. The skin is moderately thick and tough, and fits loosely, being only attached to the underlying muscles here and there. A vertical section through the skin shows it to be composed of two very clearly defined layers, an outer or **epidermis,** and an inner or **dermis.** The outer forms an **epithelium,** that is to say, a sheet of cells covering a free surface, and is compound or composed of a number of layers of cells. The cells of the various layers differ in form, according to their position. The cells at the inside are columnar in shape and granular, forming a layer known as the **Malpighian layer.** Above this the cells are polygonal, becoming more and more flat, until the outer layers are thin scale-like cells. In addition to the flattening the protoplasm of the cells undergoes modification, and is progressively replaced by a substance, keratin, allied to horn, so that the outermost cells are practically nothing but thin dead horny scales. The outer layer is cast off periodically, a process known as sloughing, and the cells are replaced by new ones produced from the Malpighian layer, which is the actively growing part of the epidermis. An epithelium thus composed of layers of cells gradually changing in character is spoken of as stratified, and although found in the epidermis of the frog is still more marked in ourselves, where the horny layer on the palms of the hands and soles of the feet is extraordinarily thick. Belonging to the epidermis are a number of hollow flask-shaped structures, the **cutaneous glands,** which dip down into the dermis. Each is composed of two parts, a spherical hollow, the **alveolus,** in the dermis lined with large cells, and a narrow tube, the **duct,** running through the epidermis and opening to the exterior. The cells lining the alveolus are, of course, epithelial, but as they are constantly engaged in forming in their

interior droplets of a substance which is afterwards passed outside, that is, they are constantly secreting, they constitute a **glandular epithelium.** Since they are only in a single layer they also form a simple epithelium. The secretion, a slimy fluid, is stored upon the alveolus and passed to the surface through the duct, and by this means the skin of the frog is kept moist. The glandular cells are

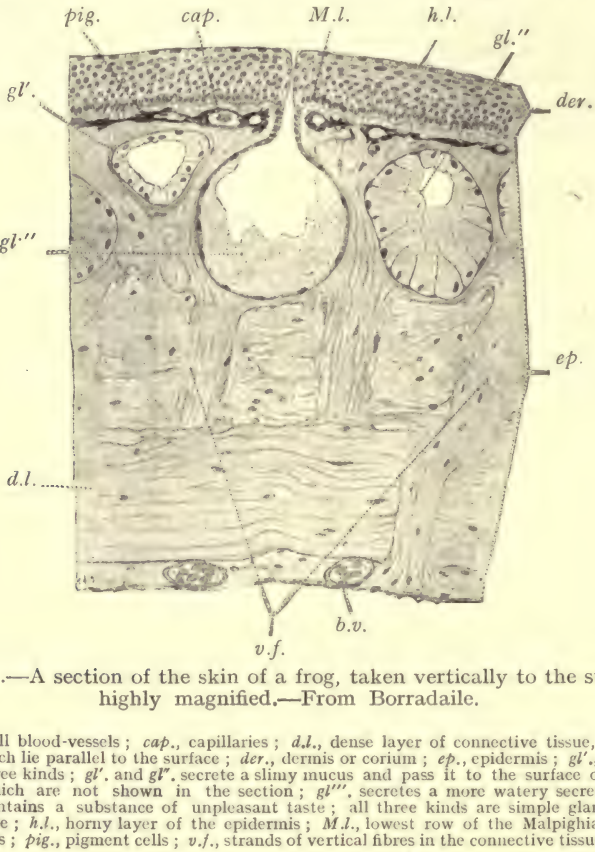


FIG. 14.—A section of the skin of a frog, taken vertically to the surface, highly magnified.—From Borradaile.

b.v., small blood-vessels; *cap.*, capillaries; *d.l.*, dense layer of connective tissue, consisting of fibres which lie parallel to the surface; *der.*, dermis or corium; *ep.*, epidermis; *gl'.*, *gl''.*, *gl'''.*, glands of three kinds; *gl'.* and *gl''.* secrete a slimy mucus and pass it to the surface of the skin by ducts which are not shown in the section; *gl'''.* secretes a more watery secretion which probably contains a substance of unpleasant taste; all three kinds are simple glands of the saccular type; *h.l.*, horny layer of the epidermis; *M.l.*, lowest row of the Malpighian layer of the epidermis; *pig.*, pigment cells; *v.f.*, strands of vertical fibres in the connective tissue.

continuous with those of the duct, but the latter are flattened and squamous instead of being almost cubical like the former. The whole is probably to be regarded as a specialised part of the epidermis that has sunk below the general level, in order to carry out its function more efficiently. Gland cells are found in many parts of an animal, and frequently close together, so as to form a glandular epithelium. When this is brought together into a definite organ we speak of it

as a gland. From their characteristic form these structures in the skin of the frog are known as **flask-glands.**

The dermis is much thicker than the epidermis, and is composed of connective tissue. Most of the fibres in it run parallel with the surface of the skin, but a certain number of strands of them run at right angles to the remainder. Unlike the epidermis the dermis has a supply of blood-vessels. They are much more plentiful than in other animals, for in the frog the skin, in addition to its other functions, plays a large part in the breathing. Immediately beneath the Malpighian layer are a number of cells deeply impregnated with granules of pigment, and another layer of more sparsely scattered pigment cells is situated deeper down. It is to the presence of these pigment cells that the skin owes its colour, and to their power of altering their shape, the possibility of altering the colour within limits. The dermis is also supplied with nerves which end just beneath the epidermis, or partly in it, in sense corpuscles, as they are termed. These are especially abundant in regions of great sensibility, such as the tongue.

The principal function of the skin is protection, and we find that it presents a tough surface to the outer world, and so guards the underlying parts from injury. The blood-vessels do not come right to the surface, so that a superficial wound does not result in a loss of blood. The skin is also protective in another sense, for its colour pattern and the power of altering it enables the animal to harmonise with its surroundings, and so avoid detection by its enemies. The second function of the skin in the frog is respiration, and so we find a large supply of blood-vessels in it, and these are not shut off from the air by such a thick layer of horny cells as we find in many animals. Then again this process is aided by the secretion of the cutaneous glands, which keeps the skin always moist, and so in a condition in which the exchange of gases can most readily take place. It is not improbable that this secretion may also help the animal to rid itself of certain obnoxious substances.

CHAPTER III

THE FROG—*RANA TEMPORARIA*—(*continued*)

Alimentary System—Respiratory System—Circulatory System—Urogenital System.

Alimentary or Digestive System.

The alimentary canal commences at the mouth, which leads directly into the buccal cavity. The structures in this, and the way in which it narrows down at the back to form an indistinct pharynx leading into the œsophagus, have already been described. The œsophagus or gullet is a wide short tube situated in the pleuro-peritoneal cavity, and attached to the dorsal wall by a mesentery. It passes on without a sharp line of demarcation into the stomach, a wide slightly curved sac lying to the left of the middle line. The walls of the stomach are very well supplied with muscles, by means of which a churning movement is maintained as long as it contains food. At the lower end of the stomach a band of circular muscles, a sphincter, is developed, by means of which the food can be retained. The position of this muscle is marked externally by a slight constriction, and the slightly swollen part of the stomach in its immediate neighbourhood is known as the **pylorus.** From this point the first part of the intestine, the duodenum, runs forward nearly parallel with the stomach, and united to it by a fold of peritoneum, the **gastro-duodenal omentum.** At the posterior end of the liver, to which it is bound by the **duodeno-hepatic omentum,** it turns sharply backwards, and is known as the small intestine or ileum. This pursues a complicated course, and is thrown into a number of convolutions all held together by mesentery, and finally it returns to the level of the hinder end of the stomach, where it swells out to form the large intestine or rectum. This runs straight backwards for just over an inch, and opens by the cloaca to the exterior. At the point where the large intestine joins the small it gives off a small dorsal projection, which may perhaps be homologous with a large sac-like structure, called the cœcum in the higher animals. The cloaca is practically the end of the intestine, but as it has connected with it the excretory and reproductive organs it is more conveniently

treated in dealing with these. The whole of the alimentary canal is lined by a thin cellular membrane, whose actual structure varies in different parts, but as it is always kept moist by secretion from some of its constituent cells, it is spoken of as the **mucous membrane** or **mucosa.**

The canal, its various parts, and the glands connected with it, are kept in position by the same peritoneum that lines the cœlomic cavity, and this is reflected round them, so as to form thin sheets of supporting tissue which bind them all together. The sheet that is attached to the original dorsal side of the canal, and runs from it to the body wall immediately beneath the vertebral column, is known as a **mesentery,** while the various side folds tying different laterally situated parts and organs to this main sheet are distinguished as **omenta.** Thus the one enclosing the liver and joining it to the stomach is known as the **gastro-hepatic omentum.**

Intimately connected with the alimentary canal are two important glands, the liver and the pancreas. The liver is a large brownish mass situated just behind the heart, and occupying a large part of the anterior end of the body cavity. It is composed of two parts, one on each side of the middle line, the right and left lobes, joined by a small connecting piece. The larger left lobe is partially subdivided into two smaller lobes. Between the two main lobes is situated a dark green spheroidal sac with thin walls, the gall-bladder, in which the gall or bile secreted by the liver is stored until required for use. Three small ducts, the **hepatic ducts,** issue from the liver substance and unite toform a common or **cystic duct,** that opens into the bladder and serves for the conveyance of the bile from the liver. Hence it is taken to the duodenum by a single tube, the **bile duct** or **ductus choledocus,** which is formed by the union of three small tubes coming from the cystic duct. This duct passes through the substance of the pancreas and some way along is joined by two or three small ducts coming from the liver. Its point of entry into the duodenum may easily be seen if the duodenum be slit up and washed out, then when the gall bladder is pressed a drop of dark green liquid will make its appearance on the wall of the intestine not far from the pylorus.

The pancreas is a pale yellow, slightly lobed, elongated gland lying between the duodenum and the stomach, slightly towards their dorsal side. It is traversed from end to end by the bile duct, into which its own numerous small ducts open, so that it acts as a common channel for bile and pancreatic fluid, and opens into the duodenum shortly after leaving the posterior end of the pancreas.

Both the liver and pancreas, as we have seen, are connected

directly with the alimentary canal, but more than this, they arise in the developmental stages of the animal as actual outgrowths of the canal, and so may be regarded as parts of it separated off and modified for special functions.

The front part of the buccal cavity is lined by a layer of very thin, flat, approximately polygonal cells, *i.e.* a **squamous epithelium.** In reality it is a stratified epithelium of many layers with squamous cells on the outside. Each cell is a very thin scale composed of coarsely granular protoplasm with a distinct granular nucleus. The various cells are held together by a certain amount of intercellular connective substance.* A number of glands open on the roof of the mouth just behind the premaxillæ, and they secrete a mucous-like substance, whose principal function is in connection with the capture of food. As the tongue is slung out of the mouth it wipes this region, and so becomes covered with sticky secretion to which the prey adheres. No glands comparable with those producing the saliva in the higher animals are present in the frog, and the digestion does not commence until the food has reached the stomach. The teeth, too, are not used for mastication, but only for holding the prey during the process of swallowing.

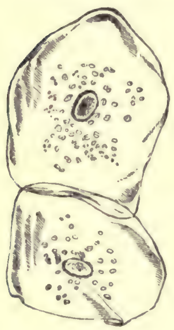


FIG. 15.—Overlapping squamous cells from the inside of the mouth. Magnified 260 diameters.—From Quain.

Further back, in the region of the pharynx, the mouth is lined by highly specialised cells. Each cell is roughly cone-shaped, with its inner pointed end resting upon a basement membrane, and possesses a large distinct nucleus within its finely granular protoplasm. The side of it turned towards the mouth is covered with a coating of very fine hair-like processes, termed **cilia,** capable of executing quick whip-like movements. The cilia are minute projections of highly-modified protoplasm, and lash sharply in one direction and then return more slowly to their initial position. Their structure and mode of action may readily be studied by examining a scraping from the pharynx of a freshly killed frog.† At the edge of the cell, just beneath the bases of the cilia, are a number of small refractive granules, and in suitably prepared material it appears as if each granule bears a cilium, and is also continued as a thin fibril into the

* More typical squamous cells may be obtained by gently scraping the inside of the human cheek with the handle of a scalpel and their structure examined by mounting the scraping in a drop of salt solution on a slide.

† Very good examples of such cells may also be obtained by teasing up portions of the gill of the mussel in salt solution.

body of the cell. The whole pharyngeal region is covered by this **ciliated epithelium,** and its constituent cells do not behave as isolated units, but act together. Bands of contraction pass over it, producing the same wave-like effect that is seen when the wind blows over a cornfield, only, of course, on a very minute scale. The purpose of this action may readily be ascertained by placing a small piece of cork on the pharynx of a frog immediately after killing; it will be slowly carried along towards the œsophagus. It will be seen, from the fact that the cilia maintain their lashing in the individual cells when separated from their fellows, that their motion is due to the activity of the protoplasm of the cell, and not to stimuli received from the nerves.

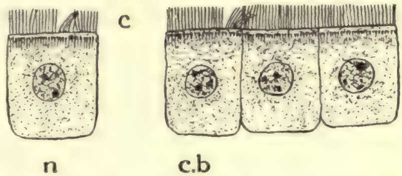


FIG. 16.—Ciliated cells; pharynx of *Rana*.

c., cilia; *c.b.*, cell body; *n.*, nucleus.

The transition from pharynx to œsophagus is marked by a change in the character of the mucous membrane, and the single-layered ciliated epithelium gives place to a many-layered compound one. This compound epithelium is in the main similar to that of the skin, its deeper cells are polyhedral and the superficial ones flat and non-ciliated. The membrane is thrown into slight folds running in the longitudinal direction, it is surrounded by connective tissue, and outside this again is a well-developed sheath of muscles, by means of which the action of swallowing is brought about. The whole is covered by the visceral part of the pleuro-peritoneal membrane.

The change to the stomach, not noticeable externally, is again accompanied by an alterntion in the mucous membrane. The slight folds become very marked and form high ridges (**rugæ**) passing along the organ. The epithelium itself takes on a glandular character, and instead of being a more or less level covering to the folds, it forms a large number of simple or branched tubes, the **gastric glands,** which sink down into the connective tissue. These do not possess the flask form of the cutaneous glands, but are test-tube shaped, and constitute examples of **simple tubular** or **compound tubular glands,** according as to whether they consist of one tube or several opening by a common duct. The cells of the single layer lining the duct are columnar in shape, with more or less clear cytoplasm and a distinct nucleus lying towards their base. In the deeper part, the **fundus** of the gland, the cells are larger and somewhat cubical. They possess a basally situated nucleus and very granular protoplasm,

the granules being termed the **zymogen granules.** In the rabbit the difference between the two types of cell is much more strongly marked, and there are present in addition certain large sub-spherical or ovoid cells. These cells are situated below the others upon the basement membrane bounding them, and, as they are regarded as being specially concerned with the production of Hydrochloric acid, they are termed the **Oxyntic cells.** Acid is also produced in the gastric glands of *Rana*, but the cells producing it are not easily distinguishable from the remainder.

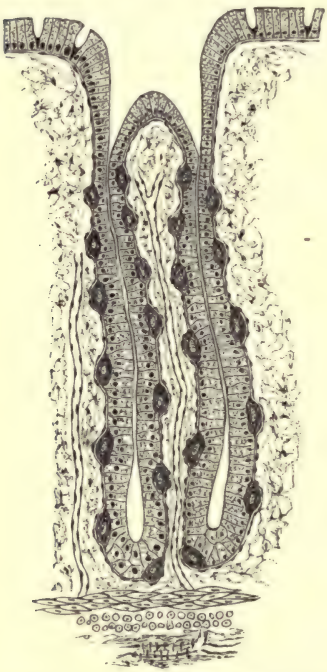


FIG. 17.—Peptic gland from the mucous membrane of the stomach. Highly magnified. —From Gray.

The function of the glands is to secrete a fluid, the **gastric juice,** that plays a very important part in the digestion of the food. In addition to the Hydrochloric acid already mentioned, it contains certain other substances that are very active chemically. They are termed ferments, or preferably **enzymes,** a name given to substances produced by living matter that are capable of producing chemical changes in other substances with which they are in contact while they remain unaltered in themselves. The enzymes appear to be derived from the zymogen granules which undergo a certain change when discharged from their cells, and their action on the food will be considered later in dealing with digestion.

The spaces between the gland tubules are filled with connective tissue, which also extends beyond them and forms a fairly thick coat, the **sub-mucosa,** plentifully supplied with blood-vessels. This connective tissue is interrupted by a very thin double circle of muscles, the muscularis mucosæ, which follow the outline of the mucous membrane. The inner part of the band is formed by circular muscles, *i.e.* muscles whose fibres run around the stomach, and the outer part by fibres at right angles to them, the longitudinal muscles. Outside the sub-mucosa is the large muscular coat of the stomach, also consisting of two parts, an inner thick layer of circular muscles and an outer much thinner layer of

longitudinal muscles. The whole, like the œsophagus, is enclosed in a portion of the pleuro-peritoneal membrane, in this case it is the peritoneum itself.

The end of the stomach is marked by the pylorus, at which point the long folds of the mucous membrane disappear, and the outer band of circular muscles becomes greatly thickened. This ring of muscles, a **sphincter,** enables the stomach to be cut off almost, if not entirely, from the intestine. The first part of the intestine is the duodenum, into which the bile and pancreatic fluid are passed. No tubular glands are present in its mucous membrane, which is not thrown into folds, but is raised into a number of small conical projections, **papillæ,** irregularly distributed. In the next part of the intestine, the ileum, the longitudinal folds again make their appearance and are closely set together. The rectum is devoid of papillæ or folds, and covered with a plain epithelium. The mucous membrane of the entire intestine consists of a columnar epithelium, whose cells have distinct, basally situated nuclei, and rest upon a basement membrane. A large number of glandular cells are to be found among the apparently unspecialised epithelial cells. These cells, called goblet cells, from the fact that they often contain a large drop of secretion at the outer end, and hence present a somewhat fanciful resemblance to a globet, do not appear to be aggregated into definite glandular areas as in the frog, as some of them are in the rabbit. The remaining layers of the intestinal wall are similar to those in the stomach, save that the muscularis mucosæ is so thin that it is often overlooked, and the sub-mucosa is very plentifully supplied with blood-vessels. The whole is encased in peritoneum. During the time that the food is undergoing digestion a slow movement of the intestinal walls is kept up. It takes the form of a series of waves of contraction, which slowly pass from pylorus to rectum, so assisting the digestive juices to mix with the food and at the same time gradually passing it onwards. As has been previously noted, this movement is termed **peristalsis,** and is brought about by the involuntary muscles of the muscular coats.

The pancreas furnishes an example of a complex gland, and is more intricate than the branched glands of the stomach. A section shows that it is composed of lobules, each consisting of a group of large granular cubical cells around a small central cavity or **lumen.** The cavities or **alveoli** of neighbouring lobules open into a small tube or duct, and these ducts join with one another and ultimately open into the bile duct. The ducts are readily detected in a section, owing to their comparatively large lumen and the flat cells forming their walls. It will be seen then that such a gland bears some resemblance to a bunch of grapes squeezed together, the ducts

represent the stalks and the alveoli the grapes, and for this reason it is termed a **racemose gland.** The glandular cells contain numerous zymogen granules, which, when discharged, give rise to the enzymes of the pancreatic juice that are utilised in digestion.

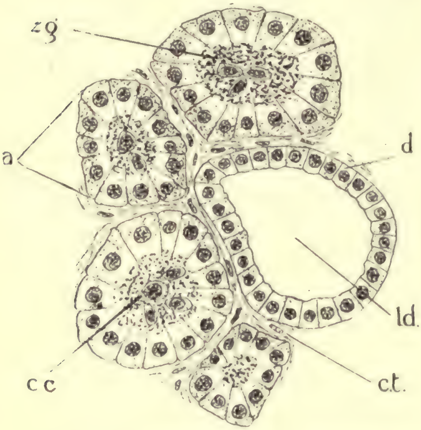


FIG. 28.—Small portion of pancreas.

a., alveolus; *c.c.*, central cells of alveolus; *c.t.*, connective tissue; *d.*, duct wall (cubical epithelium); *l.d.*, lumen of duct; *z.g.*, zymogen granules.

The liver, the largest gland in the body, is also a complex gland. It arises as a compound tubular gland, but during its growth the various tubes unite with one another into a close reticulation, so that in the adult its structure is difficult to make out. In section it is seen to consist of large numbers of polyhedral cells with distinct nuclei embedded in granular cytoplasm. It has also a very plentiful supply of blood-vessels. Here and there ducts of different sizes will be seen, and masses of pigment are irregularly distributed in it. The functions of the liver are three in number. In the first place it secretes a fluid, the bile, that takes part in the digestive processes. This bile is collected by numerous small ducts, and thence taken to the cystic ducts. The second function is the storage in its cells of a substance, **glycogen** or animal starch. The various sugars obtained from the food are brought to the liver by the blood, and there transformed into glycogen, which is insoluble. When sugar is again required by the blood the glycogen is re-converted into soluble sugar and given up to the blood. By this means the proportion of sugar in the blood is kept fairly constant, and the liver acts as a storehouse in which the excess may be kept until required. Sugar and substances of a similar chemical nature, the carbohydrates, play an important role in supplying the energy necessary for the bodily activities. The third function of the liver is connected with the removal of waste matter from the system. Certain of the waste products are brought to the liver by the blood, and there transformed into a substance called **urea.** This is secreted back again into the blood, whence it is eliminated by the kidneys.

Digestion.

We must now turn our attention briefly to the actual process of digestion itself, and in doing so we shall consider this process in general, and not in the frog in particular. The chief point of difference between the process in the frog and the rabbit is that the former does not possess any salivary glands, and hence the digestion does not actually commence in the mouth. In correlation with this we find that the frog does not masticate its food. Whether the animals considered be carnivorous, *i.e.* flesh-eating, or herbivorous, *i.e.* plant-eating, the reactions are fundamentally the same, for although the actual food substances differ slightly in the two cases they are closely allied chemically. The food taken in consists of matter that is, or has been, living, and the greater part of it falls into a small number of groups of substances, sometimes spoken of as the **proximate principles.** One most important constituent of all food is water, in addition to which we find :

1. Mineral salts, such as common salt, etc.
2. Proteins, *i.e.* compounds formed by living matter and containing Nitrogen. Ultimate analysis shows them to contain Carbon, Hydrogen, Oxygen, Nitrogen and Sulphur in various proportions.
3. Fats, *i.e.* compounds of fatty acids with Glycerine.*
4. Carbohydrates, *i.e.* compounds of Carbon, Hydrogen and Oxygen, in which the last two are in the same proportion as in water.†

The first group contains inorganic substances, and the last three organic, that is to say, substances that in nature only occur in connection with living matter. Nearly all of them are in solution, or readily soluble. Matter in solution falls into two classes, according as to whether it can or cannot pass through an organic membrane. If a vessel be divided into two compartments by means of an organic membrane (*e.g.* parchment), and a solution of common salt be poured into one side and ordinary water into the other, it will be found after a time that salt is present in both compartments. It will continue to pass through the membrane until the solution on both sides is of equal strength. Such a passage is termed **osmosis** or **dialysis,** and a compound capable of performing it is distinguished as a **crystalloid,** as such substances are usually easily obtainable in a crystalline condition. The other class of substances would be quite

* The fatty acids are a series of acids derived from the oxidation of monotomic alcohols.

† This definition is convenient rather than accurate, for while including the Carbohydrates it also includes a few compounds like acetic and lactic acids that are not carbohydrates.

unable to pass through the membrane in this manner, and are termed **colloids.**

We have already seen that the alimentary canal is a complicated tube running from mouth to anus, but nowhere opening into the body itself. The food then, in order to be utilised by the animal, must find its way into the tissues through the walls of the canal, but these walls consist of living cells, and hence form an organic membrane. Some constituents of food are insoluble, and of the remainder only the mineral salts and certain of the carbohydrates are crystalloids, while the remainder of the carbohydrates, the fats, and the proteins are colloids. The problem confronting an animal when its food is secured therefore is, how can the insoluble substances be made soluble, and how can the colloids in solution be converted into crystalloids so as to pass through the gut wall ? In order to effect the necessary changes, we find in the higher animals a complex system of glands has been evolved, and the food is subjected to the action of a number of different substances produced by them. The various alterations undergone by the food up till the time it passes into the wall of the canal are all included in the term digestion.

It is beyond our scope to enter into the details of the chemical changes brought about by the enzymes in the digestive juices, but a consideration of a few of the more important will serve to illustrate their general mode of action. The principal ones act by **Hydrolysis,** *i.e.* they cause the molecules of the substance to decompose or undergo cleavage by a reaction with water.* They may be separated into protein-splitting enzymes, starch-splitting enzymes, fat-splitting enzymes, sugar-splitting enzymes, and so on, according to the material upon which they act.

Digestion commences in the mouth by the action of the **ptyalin** of the saliva attacking and splitting up the starchy food. It is continued in the stomach where, in addition to encountering the hydrochloric acid, it is acted upon by the two ferments, **pepsin** and **rennin,** which are present in the gastric juice. The former acts upon proteins, breaking them down to simpler substances, peptones, and the latter coagulates milk. The food now, after mastication and partial digestion in the stomach, assumes a batter-like consistency and gives an acid reaction to litmus. In this condition it is termed **chyme.** After it has been thoroughly acted upon by the gastric juice it is passed on to the duodenum, and here comes under the influence of the bile and pancreatic juice.

* Thus, for example, one carbohydrate, maltose, is transformed into another, dextrose, by the action of the enzyme maltase—

$$\underset{\text{(maltose)}}{C_{12}H_{22}O_{11}} + H_2O = \underset{\text{(dextrose)}}{C_6H_{12}O_6} + \underset{\text{(dextrose)}}{C_6H_{12}O_6}.$$

Bile is in part an excretion, and conveys out of the body certain waste materials derived from hæmoglobin. Separately it has practically no digestive action, though in the body it greatly augments the action of the pancreatic juice, more particularly in regard to its action in fat-splitting, and its salts help in emulsification.

Pancreatic juice is a far more active digestive agent, and, in addition to being alkaline, contains three principal ferments. **Trypsin** is an enzyme splitting up the peptones to amino-acids, and this has much the same action as pepsin in breaking down proteins, save that it acts in an alkaline solution.* **Amylase** is a starch-splitting enzyme that is more active than the pytalin of the saliva. **Lipase** acts upon certain fats, breaking them down into glycerol and fatty acids, which, in their turn, unite with the alkali present in the pancreatic juice to form soap. The soap acts upon the remaining fats in a mechanical way, aided also by the bile salts, and forms an emulsion, *i.e.* a white milky-looking fluid, formed by minute fat globules being suspended in a liquid. The result of these various actions is that the food, having of course an alkaline reaction, is of the consistency of milk, and is now termed **chyle.**

During its passage through the remaining part of the intestine **ereptase** continues splitting up the amino-acids, the various digestive processes are completed, and the food is taken up or absorbed by the walls. The colloids, now transformed into crystalloids, pass through the mucous membrane by osmosis into the underlying blood-vessels, and are thus distributed to various parts to be utilised in the general anabolism. The fats, however finely emulsified, remain colloidal, and it appears as if the cells of the intestinal wall actually take the small globules in and pass them out at their inner end into special vessels, the **lacteals.** These vessels, with similar ones in all parts of the body, form an auxiliary part of the circulatory system known as the lymphatic system, and are specially numerous in the intestinal walls.

A certain amount of insoluble matter is always taken in with the food, and this, together with the undigested residue, accumulates in the rectum as more or less solid pellets, the fæces, which are discharged as excreta from time to time. It is noticeable when comparing an herbivorous animal, such as the rabbit, with a carnivore, like the frog, that the intestine is a great deal longer

* The action of trypsin is dependent on the presence of another substance, **enterokinase,** which is produced by the mucous membrane of the duodenum when it is acted upon by an acid. The very pancreatic fluid itself is not secreted until a substance, **secretin,** is made by the mucosa of the duodenum and conveyed to the pancreas by the blood. Indeed, the digestive actions in this part of the gut are too complex to be adequately dealt with here.

relatively to the size of the animal, and the amount of excreta is also greater in the former.

We have seen then that the alimentary canal is a long tube, whose various regions are modified for different purposes. With it are connected glands, which arise in embryonic life as outgrowths from its walls, each of which produces a specific substance or substances, termed enzymes, playing definite parts in the splitting up of certain colloidal compounds. The whole system acts together for the digestion and absorption of the food, in order that it can be utilised by the body.

Respiratory System.

Attention has already been directed to the slit-like opening at the back of the floor of the mouth, known as the glottis. It is situated upon a slight median elevation lying between the posterior cornua of the hyoid plate, and it leads into a space, the **laryngo-tracheal chamber,** or, more briefly, the larynx, whose walls are supported by cartilages. The cartilaginous structures are five in number, a complex ring-like cartilage, the **cricoid,** runs around its median walls, while the roof of it is supported by a pair of semi-lunar cartilages, the **arytenoids,** and at the middle of the inner edge of each of these is a small cartilage, the **pre-arytenoid.** It is these two pairs of cartilages that project slightly into the buccal cavity, and between them lies the glottis. Two flat bands of connective tissue, the **vocal cords,** related to the cartilages, stretch across the laryngo-trachial chamber, leaving between them a somewhat long and narrow opening, the **rima glottidis.** They can be approximated by means of a special set of muscles, and so enable the frog to croak by expelling the air from the lungs sharply through the reduced opening. The volume of sound thus produced is increased in the male by the presence of two bags, the **vocal sacs,** in the floor of the mouth, which can be inflated with air and so act as resonators. They are particularly well developed in *R. esculenta.* The laryngo-tracheal cartilages are provided with a series of muscles, by means of which the glottis can be closed, while food is being swallowed, and opened, and the chamber distended during the taking in of air, and so on.

The laryngo-tracheal chamber leads directly into the lungs, a pair of dark-coloured, thin-walled sacs lying far forward in the body cavity on its dorsal side near the heart. The lungs, like the digestive glands, arise during early life from the wall of the alimentary canal. At first they are represented by a single outgrowth from the floor of the pharynx, but as this grows backwards it splits into two. Their original connection with the pharynx is retained as the glottis.

Each lung is an oval sac with a pointed posterior end, with extremely elastic walls, and usually is found in a collapsed condition. It may, however, be inflated easily by means of a blowpipe inserted into the larynx. The interior is divided up by a network of partitions into a number of chambers incomplete at their inner ends. These in their turn are sub-divided into a larger number of smaller cells, the alveoli, by a multitude of smaller partitions.

The act of breathing is somewhat complex, and differs from that in man. The frog possesses no ribs whereby it can increase the size of the chest cavity and so cause the air to rush in ; on the contrary, the lungs are highly elastic and tend to expel the air, which, therefore, has to be forced into them. The forcing is carried out by the floor of the mouth in conjunction with certain valves in the nostrils. Internal and external nares are connected by a continuous passage, allowing of easy ingress and egress of air when not closed by the valves. Three stages can be recognised in the process: firstly, **aspiration,** during which air is drawn in through the nostrils by means of lowering the floor of the mouth, the glottis being kept closed ; secondly, **expiration,** when the contraction of the trunk muscles and the elasticity of the lungs expel some of the air from the lungs through the glottis, now open, into the buccal cavity ; lastly, immediately following upon the foregoing, **inspiration,** in which the mixed air is pumped into the lungs by raising the floor of the mouth and at the same time keeping the nares closed. It is obvious from this that the air breathed into the lungs is not fresh, but a mixture of pure air taken in through the nostrils with impure air that has already been in the lungs. If a living frog is observed it will be noticed that the floor of the mouth is constantly being moved up and down, these movements being concerned with respiration.

The lungs are extremely well supplied with blood-vessels whose smallest branches ramify in a close network in the walls of the alveoli. They are covered only by the alveolar epithelium, which is composed of a single layer of flattened cells, and so the blood in them is only separated from the air by their own very thin walls and the alveolar epithelium. Thus the oxygen in the air is enabled to diffuse into the blood, where it forms an unstable compound with the colouring matter of the blood, and in this condition is carried to the tissues, where it is utilised to release energy by the oxidation of certain substances. In this way the carbonic acid gas, one of the main products of the oxidation process, that has been collected up from the various parts and dissolved in the fluid portion of the blood is able to pass from it into the air in the lungs, whence it is expelled.

This taking in of oxygen from the air and giving off of carbonic

acid gas from the blood constitutes respiration and the exchange of the two gases is termed the respiratory exchange.

Some authorities maintain that the mere osmotic interchange of gases just outlined is not sufficient to account for the total amount of gases taken up and given off, and suggest that the alveolar epithelium also plays a part in it by actually absorbing the gas from the one side and passing it through to the other.

The lungs are the principal centre of respiration, and in the higher animals the only places where it occurs. In the frog, however, this respiration, *i.e.* **pulmonary,** is supplemented by two other kinds. The small blood-vessels in the skin are much larger than in other animals and come near to the surface, which is always moist, and so allow of a **cutaneous respiration.** Again, the vessels in the wall of the pharynx and buccal cavity give off curious sac-like diverticula, which lie between the epithelial cells lining those regions. This brings the blood into contact with the air, and a **buccal** or **pharyngeal respiration** occurs. These two last forms of respiration are peculiar to the Amphibia, the class to which frogs belong, among the Vertebrates, and are not equally important in all members of that class.

Respiration is the exchange of carbonic acid gas in the blood for oxygen in the air, and is carried out mainly by osmosis in the very vascular lungs. The exchange is aided by a force-pump action of the floor of the mouth, and in Rana is supplemented by similar exchanges in the skin and lining of the mouth and pharynx.

Circulatory System.

The circulatory or vascular system of a vertebrate consists of a series of tubes by means of which the blood is carried round the body. The central point in this system is the heart, an elaborate structure which pumps the blood into the blood-vessels, and by means of series of valves causes it to keep circulating in the same direction. Its position in the pericardium and the main vessels connected with it have already been noted. The large trunks conveying blood away from the heart are termed the arteries, and these break up into smaller and smaller branches as they get farther from the heart. The smallest of these are termed **arterioles,** and they penetrate into all the tissues of the body. In the tissues they break up into an interlacing network of very minute vessels with extremely thin walls, the **capillaries,** which unite again to form somewhat larger vessels, the **venules.** These in their turn unite to form larger and larger trunks carrying the blood back to the heart, these are the veins.

The heart, then, may be regarded as the centre of the vascular system which, as we have seen, is a closed series of tubes. It consists of five chambers, a **sinus venosus,** two **auricles,** a **ventricle** and a **conus arteriosus.** As has already been noticed, it is situated far forwards in the body in front of the main mass of the liver, and ventral to the lungs. Around it is a more or less closely fitting bag, the pericardium, composed of a white, glistening, semi-transparent membrane that is reflected back and covers the heart very

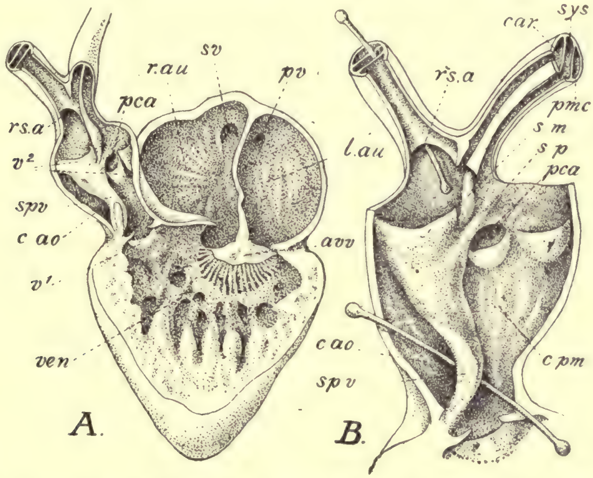


FIG. 19.—A, The frog's heart dissected from the ventral surface. B, an enlarged semi-diagrammatic view of the truncus arteriosus; the ventral wall has been cut through somewhat to the observer's right of the middle line, and the walls have been turned back.—From Bourne.

avv., auriculo-ventricular valve, with its cordæ tendineæ; *c.ao.*, cavum aorticum of the truncus arteriosus; *car.*, carotid artery; *c.pm.*, cavum pulmonale of the truncus arteriosus; *l.au.*, left auricle; *p.ca.*, opening of the pulmo-cutaneous arches into the cavum pulmonale; *pmc.*, pulmo-cutaneous artery; *pv.*, opening of the pulmonary vein into the left auricle; *r.au.*, right auricle; *r.sa.*, opening of the right systemic artery; in B a rod is passed up the opening and projects from the cut end of the middle or systemic channel of the right aortic arch; *s.m.*, septum medium of the upper part of the truncus; *s.p.*, septum principale; *sp.v.*, spiral valve, in B the reference line points to the surface of attachment to the ventral wall of the truncus which has been cut through; *sv.*, opening of the sinus venosus into the right auricle; *sys.*, systemic artery; $v.^1$, proximal row of semi-lunar valves guarding the passage from the ventricle into the truncus; $v.^2$, distal row of semi-lunar valves in the truncus; *ven.*, ventricle.

intimately. Thus the heart comes to lie in a specially separated part of the body cavity.

The sinus venosus is a dark-coloured thin-walled sac lying on the dorsal side of the heart; it is triangular in shape, with the apex pointing backwards and into its three corners open the three main veins of the body, the **Venæ cavæ** or **Caval veins.** It opens into the right auricle by a fairly large transverse slit whose edges are guarded by valves, the **sinu-auricular valves,** which allow the blood to pass from sinus to auricle, but not in the reverse direction.

The two auricles together form a large dark hemispherical sac, with thin walls, often termed the **atrium,** lying immediately in front of the ventricle from which it is separated by a deep furrow, the **coronary sulcus.** This sac is completely divided by a vertical partition, the **inter-auricular septum,** into two chambers, a large right and a smaller left auricle. The right communicates with the sinus, as already noted, and into the left opens the common **pulmonary vein** formed by the union of the two pulmonary veins, one from each lung. The two auricles open into the ventricle by a single aperture, the **auriculo-ventricular aperture,** which is partly divided by the posterior free edge of the septum. The opening is guarded by two auriculo-ventricular valves, one dorsal and one ventral, which stop the blood flowing from ventricle to auricle. These are two membranous flaps whose free edges are tied to the wall of the ventricle by a number of tough tendinous cords, the **chordæ tendinæ,** and are so enabled to withstand the pressure of the blood during the contraction of the ventricle.

The ventricle is a moderately elongated pinkish structure bluntly pointed at its posterior end. A horizontal cut shows it to have a comparatively small cavity surrounded by very thick muscular walls. The walls appear spongy, owing to the presence of a number of interlacing projecting muscular ridges between which the ventricular cavity dips deeply. This sponginess of the ventricular wall plays a part in the separation of the two different sorts of blood brought to the heart.

The Conus arteriosus is a fairly stout tube, with walls composed of cardiac muscle, which arises from the anterior ventral corner of the ventricle on the right and runs forward obliquely towards the left on the ventral surface of the atrium. Its exit from the ventricle is guarded by three **semi-lunar valves,** *i.e.* valves shaped something like small watch pockets, whose free edges can meet in the lumen and stop the blood returning to the ventricle. Within it is a spiral fold of membrane, and its anterior end, marked by another set of three semi-lunar valves ; it is continued into a small terminal portion, the **truncus arteriosus,** forming a common chamber from which two branches are given off. Each of these is divided internally into three ; the **carotid** in front, the **systemic** in the middle, and the **pulmo-cutaneous** behind, which soon manifest themselves externally as three separate arteries. These three arteries on each side constitute the aortic arches. By some authors the conus is termed the pylangium, and the truncus the synangium, quite superfluous terms.*

* Considerable confusion exists in the way these terms are used in text-books. The term conus arteriosus (**bulbus cordis** or pylangium) should be

The spiral fold or valve within the conus is a flap of membrane running obliquely and spirally forwards, practically dividing its lumen into two passages. It begins on the ventral side near the right semi-lunar valve of the posterior series, and, for the most part, attached on the dorsal side with its ventral edge free, it ends on the dorsal side of the conus near the large right semi-lunar valve. Owing to the way in which it is attached, the cavity of the conus is divided into a right channel, the **cavum aorticum,** which leads off directly from the ventricle and a left channel, the **cavum pulmo-cutaneum,** not directly continuous with the ventricle.

The truncus is divided by a horizontal septum into dorsal and ventral compartments. The dorsal chamber at the one end communicates with the cavum pulmo-cutaneum by an aperture guarded by one semi-lunar valve, and at the other passes over on each side into the pulmo-cutaneous artery. The ventral chamber is continuous with the cavum aorticum, and is further subdivided by a median vertical partition, the **septum medium,** into a right vacity which leads into the right systemic arch, and also the two carotid arches and a left chamber which leads into the left systemic arch.

Arterial System.

The arteries of the body, forming the arterial system, all arise from the three arches coming off from the truncus arteriosus, namely, the carotid, the systemic and the pulmo-cutaneous. While still united in a common trunk they pass outwards round the œsophagus for a short distance before dividing into separate vessels.

The **Carotid Arch,** soon after becoming separate, gives off a branch, the **external carotid** (often termed the **lingual**), which supplies the tongue, lower jaw and hyoid apparatus, and then swells out to form an enlargement, the so-called carotid "gland," in which the carotid breaks up into a considerable number of small vessels which reunite to form the **internal carotid** artery. This "gland" is the remains of a vascular connection present in the tadpole, and it is suggested by some authorities that it plays a part in the regulation of the blood pressure in the carotid arch. The internal carotid runs outwards and upwards to the base of the skull, where

applied in the frog to that part of the heart marked off at each end by the semi-lunar valves. Its walls are composed of cardiac muscle, it is rhythmically contractile, and it is homologous with the similarly named portion of the dogfish heart. For some reason or other it has been erroneously termed in some books, truncus arteriosus. The truncus arteriosus (pylangium), however, is merely the terminal chamber, and represents in a very abbreviated form the **Ventral aorta** (truncus arteriosus or truncus aortæ) of the dogfish. The possession of a short truncus arteriosus makes the heart of Rana intermediate between that of Scyllium, where it is long, and that of the rabbit, where it is absent altogether.

it divides into a **palatine** branch, supplying the palate, part of the œsophagus and the orbit, and a **cerebral** branch which passes through a foramen in the base of the skull and spreads out over the brain.

The **Systemic Arch** runs on laterally around the œsophagus to unite partially with its fellow of the opposite side, and so give rise to the **dorsal aorta,** the main arterial trunk of the posterior part of the body. During its passage around the œsophagus the systemic arch on each side gives off a number of branches. The **laryngeal** and **œsophageal** are two fairly small twigs, supplying the larynx and the œsophagus respectively. They are followed by the **occipito-vertebral** artery, a short trunk that divides into the **occipital,** running forwards to the back and sides of the head, and the **vertebral,** which runs back parallel with the vertebral column and gives off branches to the muscles of the back and to the spinal cord. The **sub-clavian** is the largest of the arteries coming off from the arch. It runs straight outwards, supplying the shoulder girdle and the fore limb.

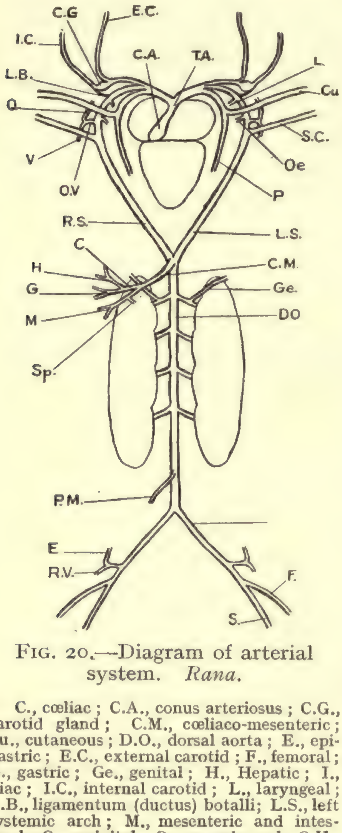


FIG. 20.—Diagram of arterial system. *Rana.*

C., cœliac ; C.A., conus arteriosus ; C.G., carotid gland ; C.M., cœliaco-mesenteric ; Cu., cutaneous ; D.O., dorsal aorta ; E., epigastric ; E.C., external carotid ; F., femoral ; G., gastric ; Ge., genital ; H., Hepatic ; I., iliac ; I.C., internal carotid ; L., laryngeal ; L.B., ligamentum (ductus) botalli; L.S., left systemic arch ; M., mesenteric and intestinal ; O., occipital ; Oe., œsophageal ; O.V., occipito-vertebral ; P., pulmonary ; P.M., posterior mesenteric ; R.S., right systemic ; R.V., recto-vesicular ; S., sciatic ; S.C., subclavian ; Sp., spermatic ; T.A., truncus arteriosus ; V., vertebral.

The two arches run together on the dorsal side of the body cavity just below the vertebral column about the level of the sixth vertebra, and the left communicates with the right by a small opening, but it is in the main continuous with the **cœliaco-mesenteric** artery, the first great branch coming off from the dorsal aorta. The cœliaco-mesenteric quickly divides into two the **cœliac** and the **mesenteric.** From the cœliac spring the **gastric** artery supplying the stomach and pancreas, and the **hepatic** supplying the liver. The mesenteric, after giving off the **splenic** to the spleen, splits into two main branches, going to the remaining parts of the alimentary canal exclusive of the end of the rectum.

The dorsal aorta then passes backwards to lie between the kidneys, to which it gives off a branch on each side that in its turn sends a **genital** artery (**spermatic** in the male and **ovarian** in the female), running to the gonad and its accompanying fat body. Immediately following this are from three to five **renal** arteries passing off to the kidneys. In this part of its course also a few short arteries, the **lumbars**, arising from the dorsal aorta, supply the muscles of the back. Behind the kidneys the dorsal aorta gives off a small **posterior mesenteric** and then divides into two large trunks, the **iliacs,** one running towards each leg. After traversing a short distance the iliac gives rise to a branch that almost immediately divides into an **epigastric,** supplying the posterior portion of the ventral body wall, and a **recto-vesicular,** supplying the end of the rectum and the bladder. Soon after this the iliac splits into a **femoral,** feeding the muscles and skin of the upper part of the thigh, and a **sciatic,** that is distributed to the remainder of the hind limb.

The external carotid artery just beyond the carotid " gland " is tied to the systemic arch by a thin strand of tissue. In the tadpole this is an open tube, and in consequence it is termed the Ductus caroticus, a similar remnant, only between the systemic and pulmonary arches, is found in mammals, and there called the Ductus Botalli, after its discoverer, Botallus.

The **Pulmo-cutaneous Arch,** the hindermost of the three, also passes round to the side of the œsophagus where the **pulmonary** artery arises and runs along on the outer side of the lung. The great **cutaneous** artery, as the trunk is now called, is a large vessel which after passing close to the ear is reflected backwards and ramifies over the under surface of the skin.

From the main arteries, briefly mentioned above, smaller arteries and ultimately arterioles arise, and so constitute a network of vessels running throughout all the various parts of the body, where, as has been noted already, they break up into minute capillaries, and so allow the blood to be distributed everywhere.

Venous System.

As we have already seen, the blood is collected up from all over the body by a series of veins which unite to form larger and larger trunks and, except the blood from the lungs, it is all returned to the sinus venosus by the three caval veins.

The **pulmonary** veins are vessels running up the dorso-lateral borders of the lungs and uniting to form a single vein which enters the left auricle immediately in front of the anterior edge of the sinus venosus.

In the same way that the arteries fall into three groups, according to the arches from which they spring, so the veins can be considered in groups according to the trunks they ultimately go to form. The veins may be dealt with in the following groups ; those contributing to the formation of the pre-caval veins, the renal portal and anterior abdominal veins and the hepatic portal vein.

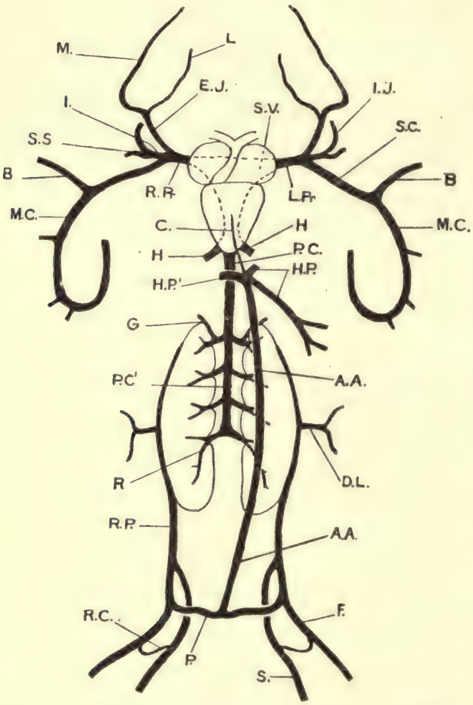


FIG. 21.—Diagram of venous system excluding pulmonary veins. *Rana.*

A.A., anterior abdominal ; B., brachial ; C., cardiac ; D.L., dorso-lumbar ; E.J., external jugular ; F., femoral ; G., genital ; H., hepatic ; H.P., hepatic portal main trunk and branch to left lobe of liver ; H.P'., branch of hepatic portal to right lobe of liver ; I., innominate ; I.J., internal jugular ; L., lingual ; L.Pr., left precaval ; M., mandibular ; M.C., musculo-cutaneous ; P., pelvic ; P.C., post caval ; P.C'., inter-renal portion of post caval ; R., renal ; R.C., ramus communicans iliacus ; R.P., renal portal ; R.Pr., right precaval ; S., sciatic ; S.C., sub-clavian ; S.S., sub-scapular ; S.V., sinus venosus.

Blood from the tongue and hyoid is collected by the **lingual** vein that runs parallel with the external carotid artery. The **mandibular** vein drains the region around the lower jaw and unites with the lingual in the neighbourhood of the carotid "gland" to form the **external jugular,** a short trunk running towards the heart.

Various tributaries from the dorsal side of the head, the eye and the brain unite near the posterior border of the orbit to form an **internal jugular** vein which passes backwards for a short distance. It is joined by the sub-scapular vein coming from the shoulder and part of the muscles of the back, and the common vessel so formed, termed the **innominate,** also goes directly inwards towards the heart.

A large vein, the **brachial,** collects the blood from the fore limb, shortly after leaving which it is confluent with the **musculo-cutaneous** vein near the shoulder joint. The musculo-cutaneous is a large vein formed by the union of a number of tributaries coming mainly

from the skin, but also, as its name implies, from the muscles of the side of the head and body. The common vein is known as the **sub-clavian,** as it is situated just inside the clavicle and it goes inwards and slightly forwards in the direction of the heart.

The external jugular, the innominate and the sub-clavian veins all unite, often at one point, but sometimes the first two join a very short distance before flowing into the third, and give rise to the **pre-caval** vein, or the **vena cava anterior.** The pre-caval vein on each side enters the sinus venosus at its anterior corner.

From each kidney arise four or five **renal** veins (**venæ renales revehentes**), and the two sets unite in the middle line to form the inter-renal portion of the **post-caval** vein, or **vena cava posterior.** Into the anterior of these renals flows a **genital** vein (**spermatic** in the male and **ovarian** in the female), coming from the gonad and fat body. The post-caval vein then runs forward, parallel with and immediately ventral to the dorsal aorta to the liver. It goes on partly embedded in the substance of this gland to which it gives no branches, but from which it receives the wide short **hepatic** vein on each side, and then enters the posterior corner of the sinus venosus.

It will be seen from the foregoing account that a number of parts of the body have not been included in those drained by the vessels entering the sinus venosus. The blood from these portions, instead of being conveyed straight to the heart, passes first by special veins to another organ, the kidney or liver, in which these veins break up into capillaries, so that both these glands have a double blood supply, venous and arterial. These capillaries are greatly distended, for which reason they are sometimes called **sinusoids,** and form comparatively large vessels with extremely thin walls, so that the blood they contain is brought into close proximity to the active secretory cells of these two organs. Such an arrangement, whereby the blood is collected up by a vein which then takes it to the capillaries of one of the organs of the body, is termed a **portal** system, so that in the frog we have **renal portal** and **hepatic portal systems.***

The blood conveyed by these systems to the organs is, of course, taken from them by the renal and hepatic veins respectively.

The blood from the hind limb is collected by two veins, the **femoral** and the **sciatic.** The femoral, returning blood from the major part of the leg, is situated on the anterior dorsal side of the thigh and runs

* The portal arrangement is not to be confused with that met with, for example, in the carotid " gland," where a vessel, usually an artery, breaks up into a network of small branches or even capillaries, but then reunites and continues as a single trunk. This is often designated a **rete mirabile.**

dorsally to the acetabulum into the cœlom. Here it divides into two branches, the external iliac vein going forward approximately parallel with the ilium, and the **pelvic vein** running ventro-mesially across the hinder part of the pelvis. The sciatic, draining the muscles and skin of the back of the thigh, runs up to join the external iliac a short distance behind the kidney. The trunk formed by this union is the **renal portal** vein, and it passes to the lateral edge of the kidney, along which it runs, gradually decreasing in calibre. Near the middle of its course along the kidney the **dorso-lumbar** vein opens into it, bringing blood from the back and lumbar region, and from it pass off a number of branches (**venæ renales advehentes**) into the kidney substance.

The two pelvics unite in the middle line on the inner surface of the body wall to form the single **anterior abdominal** vein, which in its forward course underlies the linea alba. Shortly after its origin it receives a well-marked tributary from the bladder, the **vesicular** vein, and a number of smaller **parietal** veins enter it on its way forward. At the level of the posterior end of the heart it passes up to the liver, receiving a small vessel, the **cardiac** vein, as it does so. It enters the hepatic portal vein as this vessel divides into two, and from just before its point of union it sends a small branch to the left lobe of the liver.

The hepatic portal vein is formed by a number of factors from the various parts of the alimentary canal, chief among which are the **intestinal,** composed of branches from the intestine and duodenum, the **splenic** from the spleen and the **gastric** from the stomach. It divides into two, one going to each lobe of the liver, and it receives the anterior abdominal just where it divides.

Lymphatic System.

While traversing the capillaries a certain amount of liquid passes off from the blood so that the tissues are bathed in this fluid, called the **lymph.** In addition to the arteries, veins and capillaries already described, there is present in all parts of the body a network of small vessels for the conveyance of the lymph, the **lymphatics,** which have extremely thin walls. They collapse very readily, and as they only contain the colourless lymph they are generally overlooked in dissection. Connected with the lymphatics are large spaces also containing lymph. It will be remembered that the skin of the frog is only loosely attached by means of septa to the underlying muscles of the body. The spaces separated from one another by these partitions form the great series of **sub-cutaneous lymph sacs.** Beneath the peritoneum and the muscles of the body wall are also lymph spaces, which communicate with the cœlom by

minute pores or stomata perforating the peritoneum. The spaces are well developed in the posterior dorsal region, where they are termed the **abdominal** or **sub-vertebral lymph sacs,** indeed so large are they that the kidneys are situate in them. On the surface of the kidney, are minute ciliated funnels leading into small veins, and so putting the lymph sacs in direct communication with the blood stream. The excess of lymph is also returned to the blood by means of two pairs of small pulsating vesicles connected with the lymphatics. The anterior pair are situated immediately ventral to the enlarged transverse process of the third vertebra and open into the sub-scapular vein. The posterior pair lie one on each side of the urostyle and open by a short duct into the **ramus communicans iliacus,** a small vein joining the femoral and sciatic veins.

The lymphatics plentifully distributed in the wall of the intestine are especially concerned with the collection of the fat obtained from the food, are always full a short time after a meal. The fat is in the form of a very fine emulsion, and so the contents of the vessels have a milky appearance, hence the lymphatics in these parts are often termed **lacteals.**

Thus the lymphatic vessels and sacs constitute a part of the circulatory system, and one that is auxiliary to the blood-vascular system.

Arteries and veins are not only to be distinguished from one another by the fact that the former convey blood to, and the latter from, the heart, but they also differ in structure.

An examination of a transverse section of an artery shows that its wall consists of three layers or coats. The outer coat or **tunica adventitia,** consists of a layer of areolar tissue through which pass a number of elastic fibres, and it is for this reason sometimes referred to as the outer elastic coat. The middle coat, the **tunica media,** is very thick and composed largely of unstriped muscles, most of which run in a circular direction, but some are longitudinal. It also contains a few elastic fibres. The innermost coat, the **tunica interna** or **fenestrated membrane of Henle,** is not so thick as either of the others, but is itself composed of three separate layers. The outer is an elastic layer, the middle a layer of fine connective tissue, the sub-endothelial layer, and the innermost is an epithelial layer, the **endothelium,** one cell deep forming the actual lining of the vessel. All these structures together give a tough elastic wall to the artery, which will remain open when cut and empty of blood.

A transverse section of a vein shows its wall to consist of the same parts as that of an artery, the only difference being the relative

thickness of the coats. The tunica adventitia is thicker, but contains a smaller number of elastic fibres. The tunica media and tunica interna are very much thinner, especially the former, and neither has so much elastic tissue. The result is that the wall of the vein is thinner and inelastic, so that when empty and cut it collapses. As an artery and a vein often run side by side, embedded in the same connective tissue, a section of this will show at a glance the structure of each and the difference between them. In the capillaries the walls are considerably reduced, and consist simply of the endothelium, thus bringing the blood into more intimate relation with the tissues.

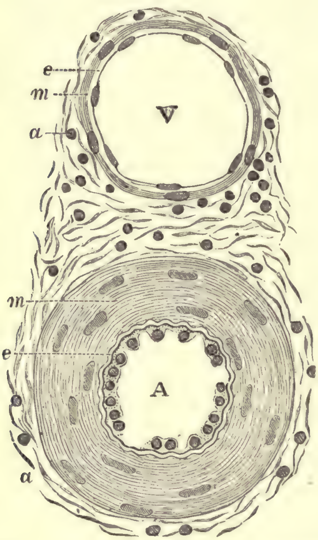


FIG. 22.—Transverse section through a small artery and vein.—From Gray.

A, artery; V, vein; *e.*, epithelial lining; *m.*, middle muscular and elastic coat, thick in the artery, much thinner in the vein; *a.*, outer coat of areolar tissue (magnified 350 diameters).

We have already seen that the blood consists of a fluid portion, the plasma, in which are suspended countless numbers of minute nucleated cells, the corpuscles. The plasma is rich in proteid matter, and one of the compounds present in it is termed **fibrinogen.** This substance, when exposed to air, as for example when a blood-vessel is cut, forms an interlacing network of threads of another and solid body, **fibrin.** The fibrin mass entangles all the corpuscles, and as it shrinks squeezes out a clear pale yellow-coloured fluid, the **serum.** This is the well-known phenomenon of clotting, and the serum represents the plasma, from which the fibrinogen has been deposited as solid fibrin threads. The corpuscles are of two kinds, colourless, the **leucocytes,** and red corpuscles or **erythrocytes.** Several varieties of the former are recognised, according to the number of nuclei they contain. They possess the power of being able to creep through the walls of a capillary without leaving a wound in it. This they frequently do, and are in consequence to be found widely distributed through the body and also in the lymph. They appear to play the part of scavengers, and help in the removal of waste matters from the tissues. In addition to this, they have the power under certain conditions of ridding the body of bacteria, and hence are of importance in helping to repel bacterial invasion—a process

termed **phagocytosis,** and the particular cells engaged in it are often called **phagocytes.** The red corpuscles owe their colour to a proteid-like substance, containing a certain amount of iron, **hæmoglobin.** This pigment plays an important part in respiration. In the capillaries of the lungs it enters into loose combination with the oxygen of the air to form an unstable compound, **oxyhæmoglobin,** of a bright scarlet colour. This blood is conveyed to the heart by the pulmonary veins, and thence by the arteries all over the body. Hence the arteries (except the pulmonary) contain bright red oxygenated blood, and such blood is sometimes termed arterial. In the capillaries of the tissues the oxygen is yielded up and hæmoglobin of a darker bluish-red colour is again produced. This is collected by the veins, so that these vessels (again with the exception of the pulmonary veins) contain a non-oxygenated darker blood, often called venous blood.

The carbon dioxide produced in the organs and tissues is on the other hand not carried in a combined form ; it simply passes into solution in the blood and lymph, and is passed out again in the capillaries of the lungs. The blood then plays an extremely important part in respiration, being the agent, by means of which the oxygen is distributed to and the carbon dioxide collected from all parts. This is but one of the functions of the blood, and in a like way it acts as a collector of food in the intestine, and then conveys it all over the body. It will also be remembered that one of the activities of the liver is to transform the nitrogenous waste matter brought to it by the blood into urea, which it returns to that fluid, so that it may be taken to the kidneys, where it is eliminated. In the warm-blooded animals, like the rabbit, the blood is also concerned with the equalisation of temperature. For example, when we are exerting ourselves the blood comes to the surface of the body, where it is slightly cooled down. The distributing power of the blood is also manifested in the transportation of certain active substances, the hormones or internal secretions, which will be dealt with more fully later.

Before leaving the blood, another very interesting form of activity, intimately connected with it, calls for attention, and that is the phenomenon termed **immunity.** It is not possible here to do more than mention one or two of its most obvious points, but it is a subject of great importance in practical medicine and interesting to the zoologist, since it is sometimes the factor determining whether or not an animal can live on a certain area. The meaning of the term is readily made clear by considering what happens when an epidemic of an infectious disease breaks out. Many persons contract the complaint severely, perhaps even fatally, others less severely, and lastly, certain persons do not catch it, however much they may

be brought into contact with infected people. These last are said to be **immune** to the disease, and those only slightly affected to be partially immune. In a similar way, one kind of animal is quite immune to diseases dangerous to others, for example, birds are not susceptible to the particular malaria common to man. These are examples of what may be termed **natural immunity** as opposed to another variety, namely, **acquired immunity.** After an attack of some diseases, like whooping-cough and chicken-pox, usually overcome in childhood, the person is not liable to a second attack, because immunity has been acquired as a result of the first attack. Immunity may also be acquired in an indirect way, by means of vaccination, as was first shown by Jenner. Thus in the case of small-pox, it has been found that if a calf is inoculated with the disease, there is produced in it a strain of germs whose virility has been very considerably lowered. These when re-inoculated into a human being are not strong enough to produce more than a temporary disturbance, but yet are strong enough to produce a measure of immunity. Most of the ill effects of these complaints are due to poisonous substances, **toxins,** produced by the organism causing the disease. When immunity has been acquired, it is found that the blood contains substances capable of combining with the toxins and rendering them inert and harmless, and these are termed the **antibodies** or **antitoxins.** The available evidence seems to show that these bodies are produced in the tissues and not in the blood, which only serves as a distributing agent. They continue to be produced long after the original stimulus has disappeared ; in some cases it may be for years. This immunity by the production of antitoxins is not limited to the effects of disease germs, for it applies also in the case of most snake poisons and some plant poisons.

Yet another kind of immunity is to be noted, and this is a most important one in the case of men living under war conditions. In this variety no antitoxin appears to be produced, but by the injection of so many million bodies of dead bacteria the tissues and fluids of the body produce a bacteriolytic substance or substances, whereby they acquire the power of being able to at once attack and digest the living bacteria, hence the disease can make no headway and the invading germs are destroyed.

The power of a man to withstand diseases is then dependent to a very large extent on this ability to produce antitoxins and **bacteriolytic substances,** and also on the readiness with which the lymphocytes will exhibit phagocytosis. The ability varies in the same individual from time to time, but may be tested by certain reactions, and what is termed an **opsonic index,** or an approximate measure of this capacity can be obtained.

Uro-genital System.

Under the present heading two systems, the excretory and reproductive, are dealt with together, not only for convenience, but also because they are closely related structurally and developmentally. The component parts of this joint system naturally differ in the two sexes, which will therefore be considered separately. The adult female has the two sets of organs separate, and so presents a somewhat simpler condition than the male.

The kidneys are two elongated, flat, oval structures of a dark red colour, lying in the sub-vertebral lymph sinus close to the vertebral column at the posterior end of the body. They are actually outside the cœlom, as they are beneath the peritoneum. Their inner edges are indented by a few notches and their outer edges intact. On the ventral surface of each is a narrow irregular strip of an orange-coloured tissue, the **supra-renal body.** From the outer side of the kidney arises a whitish tube, the **ureter,** which becomes free a short distance from its hinder end and runs straight backwards to open into the end of the alimentary canal. The two ureters open on small papillæ situated close together on the dorsal side of the terminal portion of the rectum, the **cloaca.** On the ventral wall of the cloaca, immediately opposite these papillæ, is the single opening of the urinary bladder. The bladder is a large bilobed, thin-walled sac, lying in the posterior ventral part of the body cavity. These various organs together constitute the excretory system.

The ovaries are two irregular masses, one on each side immediately ventral to the kidneys. They are attached to the dorsal wall of the cœlom by two folds of the peritoneum, known as the **mesovaria.** The presence in the ovaries of a large number of spherical eggs, like small shot, each half black and half white (during a large part of the year) renders them very conspicuous. Each egg is enclosed in a tightly fitting sac composed of a simple layer of cells, and termed the follicle. To the front end of each ovary is attached a number of finger-shaped lobes of yellow or orange-coloured fat, these are the so-called fat bodies or **corpora adiposa.** A long coiled tube, the **oviduct,** is situated laterally to the kidneys on each side of the dorsal wall of the body cavity, from which it is suspended by a fold of the peritoneum, the **mesometrium.** The front end of the oviduct forms a wide funnel-shaped opening, the **oviducal funnel,** lying far forwards dorsally to the liver. Immediately behind this the duct is a slender tube, which, however, soon becomes larger, owing to the fact that its walls become very glandular, and pursues a very convoluted course to the level of the hinder end of the kidney. Here it widens out to form a large thin-walled sac, the **ovisac,** which opens

into the cloaca. These oviducal openings appear as slit-like apertures in the dorsal wall of the cloaca, just in front of the openings of the ureters. Thus the cloaca of the female frog possesses five pores

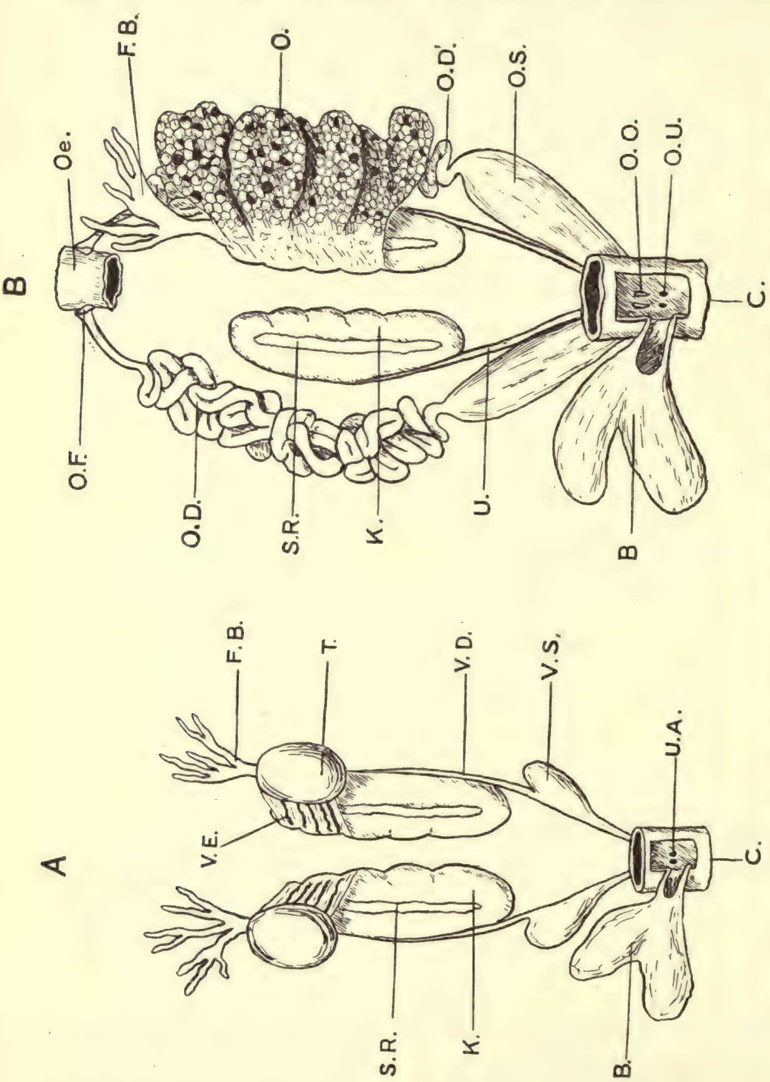


FIG. 23.—Diagram of urogenital system, *Rana*, with bladder displaced to right side. A, male; B, female with right ovary removed.

B., bladder; C., cloaca; F.B., fat body; K., right kidney; O., ovary; O.D., oviduct; O.D'., lower end of left oviduct; Oe., œsophagus; O.F., oviducal funnel; O.O., opening of ovisac; O.S., ovisac; O.U., opening of ureter; S.R., supra-renal body; T., testis; U., ureter; U.A., urogenital aperture; V.D., vas deferens; V.E., vas efferens; V.S., vesicula seminalis.

leading into it: a pair of genital openings, a pair of urinary openings, and the opening of the bladder. When ripe the eggs are discharged from the ovaries into the cœlom, and find their way forward to the

oviducal funnels, into which they are taken. They then pass along the oviduct, where they are coated with albuminous matter, to be stored in the ovisac until they are finally laid. All these parts of the female reproductive system are subject to variations at different times of the year. During the summer they are smallest, but the fat bodies enlarge. In winter, and particularly in the early months of the year, the ovaries enlarge very markedly, while the fat bodies begin to dwindle in size, yielding up their food store to the ovaries to enable them to produce an enormous number of eggs. Shortly after the glandular portions of the oviducts begin to increase in size, their glands becoming active and preparing the albuminous matter with which the egg is surrounded as it passes down the ducts. Finally, in early spring the ova are discharged and stored in the ovisac, so that the ovary diminishes markedly, and the ovisacs become greatly distended with the waiting eggs. After the eggs are laid the various organs all become smaller again.

The primary male organs are the testes, a pair of yellowish white oval bodies, lying immediately ventral to the kidneys, and suspended in folds of the peritoneum often deeply pigmented, known as the **mesorchia.** To their front ends are attached corpora adiposa, similar in all respects to those of the female. Each testis is connected to the corresponding kidney by ten or a dozen fine white tubes, the **vasa efferentia,** running through the mesorchium. The spermatozoa produced in the testes are not discharged into the body cavity, as are the ova from the ovary, but are conveyed to the kidney by the vasa efferentia. The kidneys resemble those of the female, and have ureters arising from their lateral edges. The ureter serves also to convey the spermatozoa to the cloaca, and so functions as a sperm duct or **vas deferens.** Between kidney and cloaca the vas deferens gives off laterally a sac-like dilatation, the **vesicula seminalis,** in which the sperms are stored until required. Thus there are only three pores leading into the cloaca of the male: a pair of uro-genital openings situated on papillæ on its dorsal wall, and the single opening of the urinary bladder on the ventral wall opposite. The various parts of the male system, *i.e.* fat bodies, testes, and vesiculæ seminales, also vary in size at different times of the year, but not to such a marked degree as the female organs.

A section of the ovary shows it to consist of a hollow sac with folded walls, from which a number of partitions pass inwards. From the walls and partitions the eggs project towards the interior. The **ovum** or female reproductive cell itself is a spherical cell, varying in size according to its stage of development, with a large vesicular nucleus situated eccentrically and containing several distinct nucleoli. The cytoplasm of the egg is extremely granular, owing to the presence

in it of a large number of spherical **yolk granules,** small masses serving as food reserves for the subsequent development of the ovum. The ovum is surrounded by a very thin homogeneous membrane, the **vitelline membrane,** and held to the wall of the ovary by the epithelium and connective tissue of the latter, which is reflected round it. It thus comes to lie in a sac composed of epithelium covered by a thin layer of connective tissue, and termed the follicle. In the course of development the egg grows larger, and one half become impregnated with a dense black pigment.

The testes are compact bodies, and section shows them to consist of a number of **seminiferous tubules,** whose walls are several cells thick. The outermost layer contains ordinary cells, showing little specialisation ; as they pass inwards, however, they become more and more differentiated, as the result of a process known as **maturation,** that will be considered in greater detail later. The innermost cells are very highly modified, consisting of a rod-shaped **head** containing the nucleus, a short continuation of this, the **middle piece,** and a long thread-like **tail,** capable of moving rapidly and forming an organ by means of which the whole cell is able to move about. These are the spermatozoa, or male reproductive cells, actively motile cells with the power of existing and swimming independently for a short time under suitable conditions.

In the breeding season both male and female frogs resort to ponds and pools, and when the eggs are ready to be laid they associate in pairs. The male takes up a position on the back of the female and clasps her tightly by means of the pads on the first finger, which have become enlarged and rough. As the eggs are laid the male pours over them the milt or spermatic fluid, in which the spermatozoa are contained. The sperm swims about actively until it reaches an egg into which it penetrates, and with which it fuses. Only one sperm can enter and fertilise an ovum, for immediately after this has taken place the vitelline membrane undergoes a slight alteration that prevents the entrance of other spermatozoa. Far more sperms are discharged than eggs, and consequently under normal conditions practically all the eggs are fertilised. They are now ready to develop into small free-swimming animals, tadpoles, which after a period of growth turn into frogs.

The kidney is composed of an enormous number of small tubes, the **uriniferous tubules,** bound together by a small amount of connective tissue richly supplied with blood vessels. Each tubule commences as a **Malpighian body,** situated near the ventral side of the kidney. This body consists of a hollow cup with double thin walls, **Bowman's capsule,** the interior of which is filled up by a **glomerulus.** The glomerulus is a rete mirable, formed by a branch

of the renal artery, which enters the capsule, breaks up into a mass of capillaries, and unties again to form a single vessel still to be regarded as an artery. From the Malpighian body the tubule runs fairly straight dorsally, and becomes much coiled near the dorsal surface. It then runs ventrally, again becomes coiled, and finally passes dorsally once more to open into a collecting tubule, extending nearly transversely beneath the dorsal surface of the kidney. Thus in a transverse section the middle portion consists of tubules cut more or less longitudinally, and on the dorsal and ventral sides of this is a strip where the coiled parts of the tubes are cut in all sorts of directions. The ventral border is easily recognised by the presence of the conspicuous Malpighian bodies, and also because the nephrostomes are situated on this side. The **nephrostomes** are ciliated funnels, that originate in connection with the urinary tubules, and are to be found as such in the young tadpole. During the course of development they lose their connections and acquire new ones with branches of the renal veins, hence serving as a means of communication between the lymph in the sub-vertebral sinuses and the circulatory system. The urinary tubules are lined by a ciliated epithelium, whose character varies slightly in different parts. The collecting tubule opens into a longitudinal canal on each side ; that on the inner edge of the kidney is called **Bidder's canal**, and that on the outer side is of course the ureter. The vasa efferentia open into Bidder's canal, and the sperms are conveyed thence by the collecting tubules to the ureter, so that they do not enter the uriniferous tubules. As already noticed, blood is brought to the kidneys by the renal portal vein, and this vessel breaks up into dilated capillaries, sinusoids, whose walls are closely apposed to the uriniferous tubules. The artery coming from Bowman's capsule, also bringing blood to the kidney, breaks up into capillaries that open into the sinusoids. Blood is carried away from these vessels by factors of the renal veins. It appears probable that the function of the capsule is to remove excess of water from the blood, while the nitrogenous waste, in the form of urea, is taken from it by the tubules.

The urinary bladder is lined by a peculiar type of epithelium, known as **transitional epithelium.** The cells are only two or three deep, fit together irregularly, and are not arranged in definite layers one above the other, as in stratified epithelium. Outside the epithelium is a muscular layer, composed of numerous strands of non-striate muscles distributed in an irregular manner, so as to form a network in a thin layer of connective tissue. The whole is enclosed in a close fitting extension of the peritoneum.

CHAPTER IV

THE FROG—*RANA TEMPORARIA*—(*continued*)

Nervous System and Sense Organs—Ductless Glands—Life History—Animals and Plants—Classification.

Nervous System and Sense Organs.

The nervous system and organs of the senses are so intimately related that they may be regarded as forming one system, whose main function is the appreciation of messages from the outside world and meeting them in the proper way. For convenience of description, we may subdivide them into the Central Nervous System, the Peripheral Nervous System, and the Sense Organs.

The **Central Nervous System** is composed of two parts, the brain, lodged within the skull, and the spinal cord, which is contained in the neural canal, formed by the neural arches of the vertebræ. The peripheral nervous system comprises three groups of structures: nerves given off from and going to the brain, *i.e.* the **Cranial Nerves,** similar nerves, the **Spinal Nerves,** related to the spinal cord, and the **Sympathetic** or **Involuntary Nervous System,** a double chain of small nerve centres lying in the cœlom close to the vertebral column. The sense organs are the olfactory organ, or organ of smell, the eye, the ear, and the organs of taste and touch.

The tissue composing the central nervous system is soft, but is of vital importance to the animal, and in consequence we find that it is not only enclosed within the bony axial skeleton, but also, inside that again, it is protected by two membranes, the **meninges.** The outermost of the membranes, the **dura mater,** is tough and pigmented, and applied fairly closely to the inner side of the bones of the skull and vertebral column. The inner membrane, the **pia mater,** corresponds to the pia mater together with the arachnoid tissue, which forms an intermediate layer in the higher vertebrates. It is richly supplied with blood-vessels, and attached to the surface of the central nervous system, the outline of which it follows closely, dipping down into all the folds. Where it covers the parts of the brain known as the optic lobes it is deeply pigmented.

The brain is an elongated mass of nervous tissue filling up the whole cavity of the cranium. It is composed of two distinct kinds of tissue, as will be seen if it is cut in section : a layer of grey matter around the outside and white matter within. Looked at from the dorsal aspect, it will be seen that the anterior half, the fore-brain or **prosencephalon,** is mainly composed of two elongated ovoidal masses, the cerebral hemispheres or **telencephalon.** These are separated from one another in the middle line by a deep groove, the **sagittal fissure.** In front the hemisphere is continued forward into the olfactory lobe or **rhinencephalon**, and these unite in the

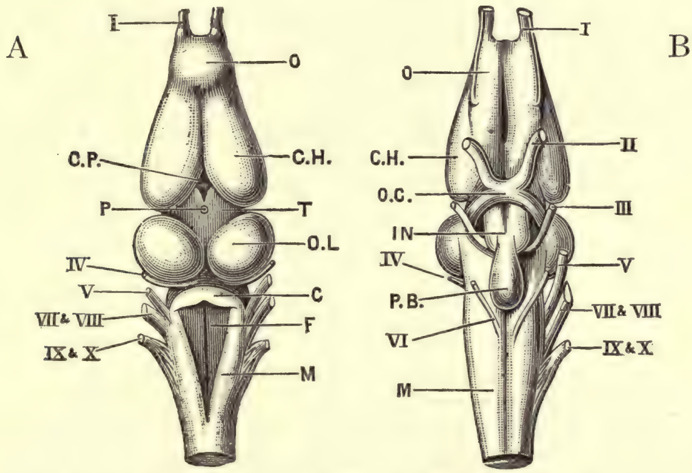


FIG. 24.—A, the brain of the frog : dorsal surface. × 4. B, the brain of the frog : ventral surface. × 4.—From Marshall and Gamble.

C., cerebellum ; C.H., cerebral hemisphere ; C.P., choroid plexus of third ventricle ; F., fourth ventricle ; IN., tuber cinereum ; M., medualla oblongata ; O., olfactory lobe ; O.C., optic chiasma ; O.L., optic lobe ; P., stalk of pineal body ; P.B., pituitary body ; T., thalamencephalon.
I., olfactory nerve ; II., optic nerve ; III., third or motor oculi nerve ; IV., fourth nerve ; V., fifth or trigeminal nerve ; VI., sixth nerve ; VII. and VIII., combined root of facial and auditory nerves ; IX. and X., combined root of glossopharyngeal and pneumogastric nerves.

middle line, so forming the anterior limit of the fissure. The posterior limit is formed by the **lamina terminalis,** the front wall of the median part of the **thalamencephalon**, as the next part of the brain is called. It is a comparatively small median portion, situated between the divergent hinder ends of the hemispheres and behind them. The top of it is fairly conspicuous in the freshly killed animal, appearing as a reddish area, the **anterior choroid plexus,** formed by a large increase in the size and number of blood-vessels of the pia mater in this region. From the posterior end of the thalamence-phalon a thin stalk runs forward over the surface of the brain, to

terminate in a small knob-like enlargement just beneath the fronto-parietal bones. This is the **pineal body** or **epiphysis cerebri**, the vestigial remnant of what was once apparently a pair of eye-like structures; it is generally removed in dissecting out the brain, but its stalk can usually be made out readily.

The succeeding part of the brain is the mid-brain or **mesencephalon.** Dorsally it takes the form of two conspicuous ovoid lobes, the **optic lobes** or **corpora bigemina,** whose long axis is inclined outwards at an angle of about 45 degrees to the median line, and over which, as already noticed, the pia mater is deeply pigmented. The hind-brain or **rhombencephalon** is divided into two portions, that in front, immediately behind the optic lobes, is the **cerebellum** or **metencephalon**, appearing as a small transversely running fold of tissue. The remaining part of the hind-brain is a good deal larger, almost as long as the cerebral hemispheres, and variously known as the bulb, **medulla oblongata** or **myelencephalon.** This again is conspicuous in the freshly killed animal, owing to the presence of a blood network, the **posterior choroid plexus,** which in the form of a long isosceles triangle covers a large part of its dorsal surface. The hinder part of the medulla is continuous with the spinal cord.

Turning now to the ventral surface of the brain, we find in front the olfactory lobes, followed by the cerebral hemispheres separated by a marked groove. The thalamencephalon is a small but an important part of the brain, and under it the nerves going to the eyes, the **optic nerves,** form a very characteristic X-shaped structure known as the **optic chiasma.** Immediately behind this is a bi-lobed swelling with a median groove, the **tuber cinereum** or **infundibulum**. It lies in the mid-ventral line and has attached to it the **pituitary body** or **hypophysis cerebri.** This is composed of a flat median cushion, immediately behind the tuber cinereum, which gives off two small lateral tongue-like processes running forward.

The ventral part of the mid-brain is formed by two large columns of nervous matter, the **crura cerebri,** that connect up the hemispheres with the **medulla** which forms the remaining part of the brain and has running down the middle of it the **ventral fissure.**

The whole of the central nervous system is hollow, and in the brain the central cavity swells out to form a series of spaces known as ventricles. The first are the ventricles in the cerebral hemispheres, an outgrowth from each of which extends forward into the olfactory lobes. The cavity of the thalamencephalon is known as the third ventricle. Its roof is formed mainly by the anterior choroid plexus, and in its nervous portion run two transverse bands of fibres, the superior and posterior cerebral commissures, joining the cortex of one hemisphere to that of the other. From its floor a pocket projects

downwards and backwards, it is termed the infundibulum and forms, when viewed from the outside, the projection on the ventral surface of the brain known as the tuber cinereum. The front wall of the third ventricle is formed by the lamina terminalis, in which runs the anterior cerebral commissure, and the lateral ventricles of the hemispheres here open by two apertures, known as the **foramina of Munro.** The fourth ventricle is situated in the medulla, and is a large cavity whose roof is formed by the posterior choroid plexus. It is joined to the preceding cavity by a passage running through the mid-brain. In the frog it is fairly large and continuous with two spaces in the optic lobes, the optic ventricles, but in the higher animals it is only a small hole, consequently it is termed the **aqueduct**

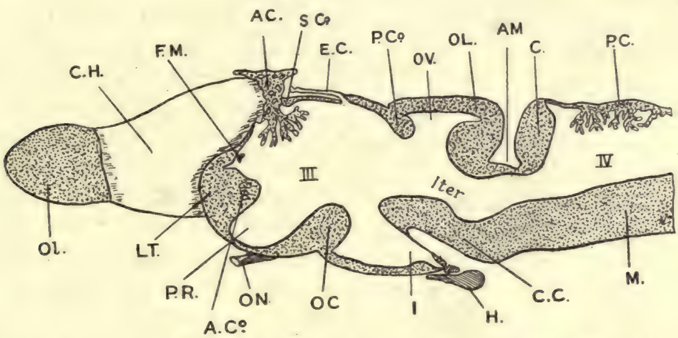


FIG. 25.—Median longitudinal section of brain, *Rana*, adapted from Gaupp.

A.C., anterior choroid plexus ; A.Co., anterior commissure ; A.M., anterior medullary velum ; C., cerebellum ; C.C., crura cerebri ; C.H., median surface of cerebral hemisphere ; E.C., epiphysis cerebri (pineal body) ; F.M., foramen of Munro ; H., hypophysis cerebri (pituitary body) ; I., infundibulum ; L.T., lamina terminalis ; M., medulla oblongata ; O.C., optic chiasma ; O.L., optic lobe ; Ol., olfactory lobe ; O.N., optic nerve; O.V., optic ventricle ; P.C., posterior choroid plexus ; P.Co., posterior commissure ; P.R., pre-optic recess ; S.Co., superior commissure ; III., third ventricle ; IV., fourth ventricle.

of Sylvius or the **Iter** (a contraction of Iter a tertio ad quartum ventriculum).

The spinal cord is a continuation of the brain and, like it, is hollow, the small cavity running through it being called the central canal or **canalis centralis.** The cord itself is a dorso-ventrally flattened, thick-walled tube situated in the neural canal of the vertebral column. It is not of uniform diameter throughout its course, but swells out in the region of the second vertebra to form the brachial enlargement, and again in the region of the sixth or seventh vertebra to form the lumbar enlargement. After this it quite sharply narrows off to form a fine thread, the **filum terminale,** which is continued on into the urostyle. It is composed of the same two substances as the brain, *i.e.* white and grey matter, but their

relative positions are reversed, for here it is the white matter that is outside and the grey matter inside. The transverse section of the cord presents a very characteristic appearance. It is approximately trapezoidal with well-rounded corners. On the dorsal side is a very shallow groove, the **dorsal fissure,** and on the ventral side is a well-marked fairly deep furrow, the **ventral fissure.** The grey matter is arranged within the white in such a way that its outline is somewhat similar, only exaggerated, and it is possible to recognise two dorsally situated blunt horns or **dorsal cornua,** and two ventral ones, the **ventral cornua.** In these, particularly in the latter, will be seen the bodies of large nerve cells. Near the middle of the section will be seen the small canalis centralis lined by a characteristic **neural epithelium.** In addition to the actual nerve cells, there are present in the spinal cord certain supporting elements known as the **neuroglia cells.**

Peripheral Nervous System.

The frog possesses ten * pairs of cranial nerves coming off from the brain, and ten pairs of spinal nerves coming from the spinal cord. Each nerve is made up of a large number of fibres bound together, and breaks up into smaller and smaller bundles as it passes away to the tissues. A nerve fibre is only capable of conveying a nervous message or impulse in one direction, consequently one set of fibres takes messages to the central nervous system, and these are termed afferent or sensory nerves, while the other set, taking messages away from the brain, are termed efferent or are spoken of as motor nerves. It sometimes happens that all the many fibres composing one nerve are of the same sort, and we then use the terms "afferent" and "efferent" to describe the nerve as a whole, while if it contains both kinds of fibres it is called a mixed nerve.

The first pair, the **olfactory nerves,** come from the front end of the olfactory lobes and are sensory, being distributed to the lining of the nasal cavities, *i.e.* the olfactory organs. The second or **optic nerves,** the nerves of sight, are large sensory nerves arising from the side of the brain beneath the optic lobes. They partly cross over to the other side on the ventral side of the brain forming the optic chiasma, and they run through the orbit into the eyeball, where they spread out over its inner surface. Surrounding them is a muscle, the retractor bulbi, which can pull the eyeball back into its orbit.

* In addition to these ten cranial nerves there are also two others, the nervus terminalis and nervus septalis, but they are very small and difficult to find. They will be dealt with more fully later in considering the Dogfish and Rabbit, and it is sufficient to simply notice their presence at this place.

The third nerve, a small motor nerve arising from the ventral surface of the brain between the crura cerebri, is distributed to four of the muscles concerned with moving the eyeball, namely, the superior and inferior recti, the internal rectus and the inferior oblique. It is termed the **motor oculi**. The fourth, the **pathetic,** is also a very small motor nerve which, arising from the dorsal surface of the brain between the optic lobes and cerebellum, runs to the superior oblique, another of the eye muscles. The sixth, or **abducens,** similarly is

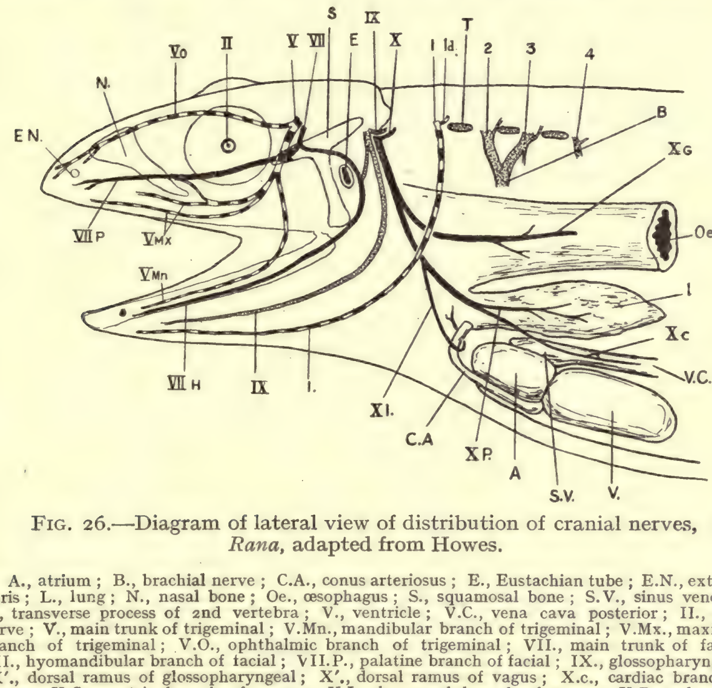


FIG. 26.—Diagram of lateral view of distribution of cranial nerves, *Rana*, adapted from Howes.

A., atrium; B., brachial nerve; C.A., conus arteriosus; E., Eustachian tube; E.N., external naris; L., lung; N., nasal bone; Oe., œsophagus; S., squamosal bone; S.V., sinus venosus; T., transverse process of 2nd vertebra; V., ventricle; V.C., vena cava posterior; II., optic nerve; V., main trunk of trigeminal; V.Mn., mandibular branch of trigeminal; V.Mx., maxillary branch of trigeminal; V.O., ophthalmic branch of trigeminal; VII., main trunk of facial; VII., hyomandibular branch of facial; VII.P., palatine branch of facial; IX., glossopharyngeal; IX'., dorsal ramus of glossopharyngeal; X'., dorsal ramus of vagus; X.c., cardiac branch of vagus; X.G., gastric branch of vagus; X.L., laryngeal branch of vagus; X.P., pulmonary branch of vagus; I., hypoglossal; Id., dorsal ramus of hypoglossal; 2, 3, and 4, second, third and fourth spinal nerves.

a very small motor nerve, but it takes its origin from the ventral surface of the medulla just behind the pituitary body. It runs to the last of the muscles concerned with the movement of the eye, namely, the external rectus.

The largest of the cranial nerves is the fifth, or **trigeminal.** It arises from the side of the medulla by two roots which unite and enlarge to form a swelling, the pro-otic ganglion, where it comes into contact with the sixth and seventh nerves, and then leaving this ganglion it passes through the skull just in front of the auditory

capsule. Outside the skull it divides into two branches, the ophthalmic and the maxillo-mandibular. The ophthalmic branch, which is mainly a sensory nerve, runs forward through the orbit along its inner side, passing above all the eye muscles save the superior rectus. At the anterior end of the orbit it divides into two main branches, one to the mucous membrane of the olfactory organ, and the other to the skin round the snout. The maxillo-mandibular branch is a short mixed nerve that passes outwards just in front of the auditory capsule and soon divides into two branches. Its maxillary branch runs forward in the lower part of the orbit below the eyeball and supplies the upper jaw, upper lip, the lower eyelid with its depressor muscle and the adjacent parts. The mandibular branch goes outwards, downwards and backwards beneath the quadrato-jugal bone to the articulation of the mandible. It passes round this and forward along the outer side of the lower jaw, to which it gives branches supplying the lower lip and skin muscles of the floor of the mouth. The fifth nerve as a whole, then, is a mixed nerve dividing into three main branches, hence its name, the trigeminal.

The seventh, or **facial nerve,** is also a mixed nerve, arising from the side of the front end of the medulla, with a distribution somewhat resembling the fifth. Like this, it runs to the pro-otic ganglion and leaves the skull by the same foramen. Outside, it at once divides into two branches, the palatine and the hyomandibular. The palatine runs forward close above the mucous membrane of the mouth in the lower inner part of the orbit. At the front end of the orbit it is joined by a cross piece, an anastomosis, to a twig from the maxillary branch of the fifth nerve. It is distributed to the mucous membrane of the front end of the roof of the mouth. The hyomandibular branch proceeds outwards around the auditory capsule, past the inner end of the columella auris, just beyond which it receives an anastomosis linking it with the ninth nerve. Thence it runs downwards in the posterior wall of the Eustachian tube, giving twigs to the tympanum, to the articulation of the mandible to which it sends twigs. Here it divides into two, one branch, the internal mandibular, runs in the floor of the mouth near the lower jaw supplying the muscles and skin. The other, the hyoidean, is larger and more posterior and passes forwards in the floor of the mouth by the side of the anterior cornu of the hyoid cartilage, supplying the skin and muscles on its way.

The **auditory nerve,** which is the eighth of the series, is a short stout nerve, purely sensory, coming from the side of the medulla just behind the seventh. It passes straight out into the auditory capsule through a special foramen and is distributed to the epithelium lining the various parts of the internal ear.

The ninth nerve, known as the **glosso-pharyngeal,** is a mixed nerve, but mainly sensory, arising from the medulla behind the eighth by roots in common with the tenth nerve. They leave the skull together by the same foramen, the jugular foramen, situated on the outer side of the exoccipital condyle, immediately before leaving which they form a large jugular ganglion. On quitting this the ninth sends a small branch forwards, which, as already noted, anastomoses with the hyomandibular branch of the seventh nerve. The remaining branch passes round the pharynx to the floor of the mouth and pursues a characteristic wavy course below and inside the anterior cornu of the hyoid cartilage. It supplies the mucous membrane of the floor of the mouth and the tongue, in which it ends.

The tenth is a large mixed nerve, called the **vagus** or **pneumogastric,** and it arises and leaves the skull in the way indicated above. It is unlike all the preceding cranial nerves in that it is distributed to structures outside the head. After quitting the jugular foramen it gives off a few twigs to the muscles of the back, and passes in the wall of the pharynx backwards and downwards, dividing into four main branches. The first, the recurrent laryngeal, loops round the pulmo-cutaneous artery and runs inwards to the larynx. The second or cardiac passes to the heart, the third or pulmonary to the lungs, and the last or gastric breaks into two smaller branches going to the stomach and other viscera.

Spinal Nerves.

There are in the adult ten pairs of spinal nerves, for although others are present in the tadpole, they disappear during the course of its development. Each nerve is mixed and arises from the spinal cord by two quite distinct fairly equi-sized roots. The dorsal root comes from the dorso-lateral aspect of the cord and is related to the dorsal horn of grey matter within it. A short distance from its origin it bears a swelling, the dorsal root ganglion, and immediately after unites with the ventral root. The ventral root is similarly related to the ventral horn of grey matter, and leaving the ventro-lateral border of the cord runs, without any ganglionic enlargement, to join the dorsal root. The common trunk so formed is surrounded by a deposition of calcium carbonate forming a conspicuous white patch, and passes out of the vertebral column through the intervertebral foramen. It divides almost at once into two unequal branches ; a small dorsal branch or ramus which runs dorsally to the muscles, and a larger ventral ramus which is the main nerve.

The first spinal nerve is known as the **Hypoglossal,** and it leaves the vertebral column by the intervertebral foramen between the first

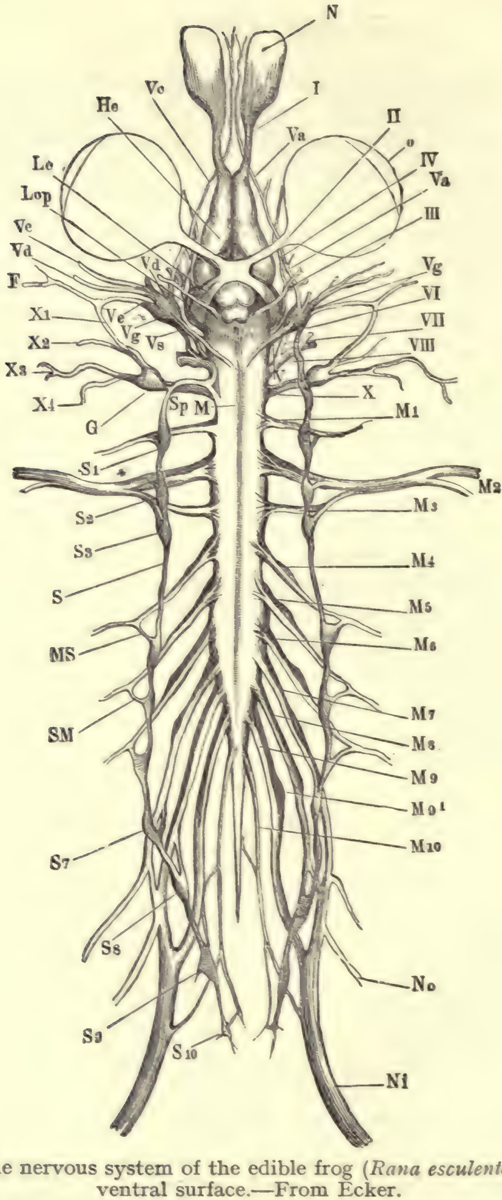


FIG. 27.—The nervous system of the edible frog (*Rana esculenta*), from the ventral surface.—From Ecker.

F., facial nerve; G., ganglion of pneumogastric nerve; He., cerebral hemisphere; Lc., optic tract; Lop, optic lobe; M., boundary between medulla oblongata and spinal cord; M. 1–10, the spinal nerves; MS., connection between fourth spinal nerve and sympathetic chain; N., nasal sac; Ni., sciatic nerve; No., crural nerve; o., eyeball; S., trunk of sympathetic; S. 1–10, the sympathetic ganglia; Sp., continuation of sympathetic into head.

I., olfactory nerve; II., optic nerve; III., motor oculi; IV., fourth nerve; V., trigeminal and facial nerves; Va., ophthalmic branch of trigeminal; Vc., maxillary branch of trigeminal; Vd., mandibular branch of trigeminal; Ve., hyomandibular branch of facial; Vg., Gasserian ganglion; Vs., upper end of sympathetic trunk, in connection with Gasserian ganglion; VI., abducens nerve; VII., facial nerve; VIII., auditory nerve; X., glossopharyngeal and pneumogastric nerves; X1., ramus anterior of glossopharyngeal; X2., ramus posterior of glossopharyngeal; X. 3–4, branches of pneumogastric.

and second vertebræ. It runs forward in the floor of the buccal cavity ventral to the glosso-pharyngeal nerve, and is distributed to the muscles of the tongue and floor of the mouth. The hypoglossal nerve in the mammals has become shifted forward and forms one of the cranial nerves, of which there are twelve in this group, and not ten as in the frog.

The second is a large nerve running straight outwards. Branches from the first and third, a small nerve, also join it, forming a complex termed the **Brachial plexus,** which supplies by a large branch, the coraco-clavicularis, the muscles of the shoulder girdle. The main trunk, the Brachial, goes on into the arm, dividing just above the elbow into radial and ulnar branches.

The succeeding three pairs of nerves, four, five and six, are small nerves supplying the skin and body wall in the trunk region.

The seventh, eighth and ninth nerves unite in a somewhat complex manner to form the large **Sciatic plexus** well outside the vertebral column. Inside the neural canal these nerves, together with the tenth and the filum terminale of the spinal cord, run downwards in a brush-like group known as the **cauda equina.** From the sciatic plexus, the exact constitution of which is subject to a certain amount of variation, come off three nerves : the ihohypogastric supplying the muscles of the abdomen, the crural supplying the muscles of the thigh and the large sciatic, which runs down the thigh and divides into tibial and peroneal branches, supplying the muscles and skin of the leg and foot. The last and smallest of the spinal nerves is the coccygeal, which leaves the vertebral column by a foramen in the urostyle and after giving a branch to the sciatic, branches over the bladder, cloaca and surrounding tissue.

Minute Structure of the Nervous System.

The structural unit of the nervous tissue is the **nerve cell** or **ganglion cell.** A typical nerve cell is very large compared with most other cells of the body, and consists of a cell body from which various processes are given off. The cell body is composed of a basis of ordinary protoplasm, which is very granular owing to the presence in it of a substance, the **tigroid substance,** in the form of small grains, **Nissl's granules.** These appear to form a store of reserve material that is utilised in the periods of activity of the cell, for far more of it is present in a cell that has been resting for some time than in a similar cell that has been very active. Appropriate staining also shows in it a number of very fine strands, the **neurofibrillæ,** which interlace freely and are continued out into the various processes, linking them up with one another in all possible directions. Near the middle of the cell is a spherical nucleus which is

fairly clear, staining but lightly and containing a well-marked nucleolus. In certain very large nerve cells a system of tiny canals seems to be present in the cytoplasm, and it is thought they conduce to the ready removal of waste products and to the supply of nutriment.

One of the processes leaving the cell differs in function from the rest ; it takes nervous messages away from the cell and is termed the

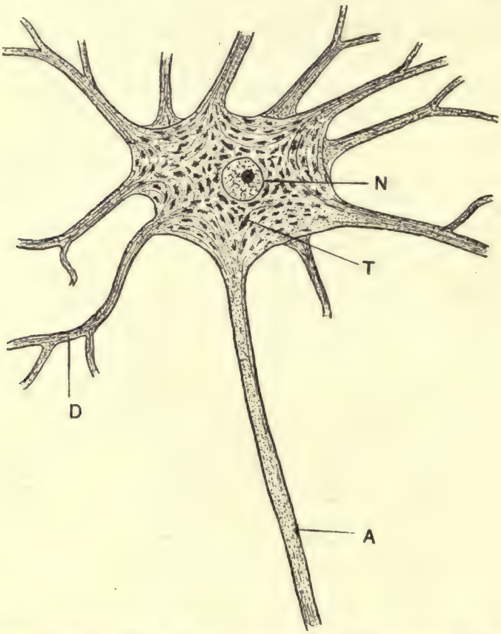


FIG. 28.—Diagram of a multipolar nerve cell from the spinal cord of an ox.

A., axon ; D., dendron ; N., nucleus ; T., tigroid substance.

axon or **neuraxis.** In many cases it differs also in structure, for it forms a long, in some parts enormously long strand of fibrillar protoplasm of practically uniform diameter. During its course it gives off a certain number of very delicate fibrils, the **collaterals,** and finally finishes up in a little tuft of twigs known as the **terminal dendrite.** This is always the case in cells whose fibres leave the spinal cord and pass out into the tissues, and they may be long enough to run right from the cord to the tips of the toes. If, on the other hand, the cell remains within the central nervous system, the axon is generally not nearly so long and resembles more closely the other processes, and its terminal dendrite is often more spread out.

The other processes coming from the cell are termed the **dendrons,** and as a rule are shorter and branch more freely, forming a tree-like structure. They are the receptive processes and convey the stimuli to the cells. The processes of various related ganglion cells come very close to one another in most cases, and in some appear to come into actual contact, so that the nerve impulses, as the nerve messages are called, can be transferred from the axon of one cell to the dendrons of other cells adjacent to it. The whole structure, cell body, dendrons and axon, is termed a **neuron,** and the nervous system is composed of countless numbers of such closely bound up together, with other cells of a supporting nature, the **neuroglia cells.** Three main types of neurons are met with and are distinguished by the number of processes given off. If but one process is present, the cell is termed unipolar. Such cells are found, but not plentifully, in the dorsal root ganglia, and as the single process divides into two branches, an axon and a dendron, they may perhaps be regarded as a specialised form of the second group. The next group are termed bipolar, as they have but one dendron in addition to the axon, and these too occur in the dorsal root ganglia. All other cells with more than two processes are termed multipolar, and are found throughout the whole of the ventral nervous system and are particularly well marked in the ventral horn of grey matter in the spinal cord. The actual form of the neuron varies in different parts, and it is possible to tell within certain limits from what part of the brain a section is taken, from the shape and arrangement of its ganglion cells.

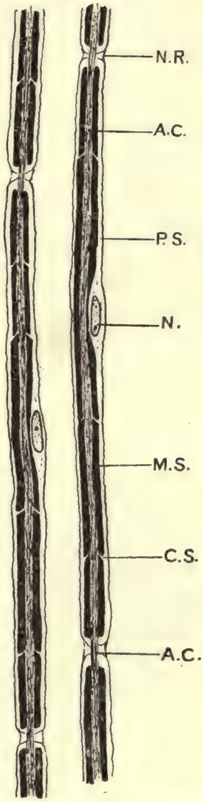


FIG. 29.—Portions of two nerve fibres.

A.C., axis cylinder; C.S., cleft of Schmidt; M.S., medullary sheath; N., nucleus; N.R., node of Ranvier; P.S., primitive sheath.

The axons and dendrons, especially if they have to travel far from the parent cell, are covered with a thin but moderately tough transparent membrane variously known as the **neurilemma,** the **primitive sheath** or sheath of Schwann. The nuclei belonging to this covering are scattered irregularly on its inner surface between it and the nerve fibre, which is termed the axis cylinder. The whole structure is of a greyish colour and is known as a grey fibre or, in

contradistinction to the second group of fibres, as a non-medullated fibre.

If the fibre is one that leaves the central nervous system it is provided with yet another protective and insulating coat. Between the primitive sheath and the axis cylinder is developed a comparatively thick layer, the **medullary sheath,** composed of a substance, myelin, closely allied to fat. This substance is highly refractive in the living condition, and consequently these nerves have a characteristic double contour when seen under the microscope, but when dead become white and opaque, and hence such nerve fibres are termed white or medullated fibres. The neurilemma is present as before, and its nuclei immediately beneath it. The medullary sheath is not continuous throughout the length of the fibre, but divided into a series of fairly long segments. In the short gaps between these segments the primitive sheath, slightly thickened, comes into contact with the axis cylinder. The ring-like constrictions formed in this way are termed the **nodes of Ranvier,** and the portion from one node to the next is an internodal segment. In the living condition the medullary sheath is apparently homogeneous and continuous in the internodal segment, but when dead it appears to break up into a series of overlapping portions, the segments of Schmidt, which are separated from one another by clear narrow fissures running obliquely to the long axis of the axis cylinder. In the higher vertebrates each internodal segment has only one elongated oval nucleus lying in the neurilemma, but in fish a number of nuclei are scattered in each internode.

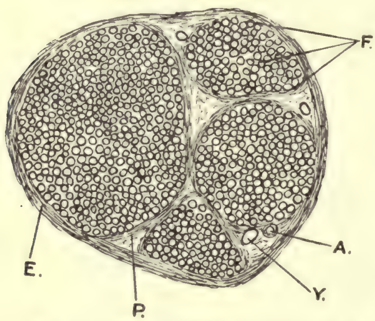


FIG. 30.—Transverse section of a nerve.

A., artery; E., epineurium; F., fasciculus; P., perineurium; V., vein.

It has already been mentioned that both brain and spinal cord are composed of grey and white matter. The grey matter is mainly composed of the cell bodies with non-medullated axons and dendrons, while the white matter is almost entirely made up of white fibres.

If a nerve such as we find in any part of the body, *e.g.* the sciatic nerve, be cut in transverse section it will be seen that it is composed of an enormous number of fibres grouped together and surrounded by a tough connective tissue envelope, the **epineurium.** Within this the fibres are seen to be arranged in definite bundles of various sizes, the **fasciculi**, each of these has its own sheath, the

perineurium, whose substance is continuous with the epineurium. Yet again, the individual fibres themselves are separated by a small amount of the same kind of tissue, here termed the **endoneurium.**

The neuroglia cells are found all through the central nervous system and are much-branched cells, whose fibrous processes connect up with one another in such a manner as to make a supporting scaffolding for the more delicate nerve cells and processes.

Sympathetic or Involuntary Nervous System.

The sympathetic system in Rana is well developed, and consists of a double chain of ganglia joined by longitudinally running strands and closely connected with both the cranial and spinal nerves. The ganglia and cords are usually covered with a layer of black pigment, which makes them easy to follow. It takes origin on each side in the pro-otic ganglion, and runs backwards in the cranium to leave it with the ninth and tenth cranial nerves through the jugular foramen. The first ganglion is formed on the postero-ventral aspect of the hypoglossal nerve, and is connected with this nerve by a few fine fibres. Thence it passes back close to the systemic arch, and then along the sides of the dorsal aorta forming eight or nine ganglia, the number is not constant, while so doing. Each ganglion is connected with its corresponding spinal ganglion by means of a nerve stalk, the **ramus communicans,** and these increase in length as they pass backwards. The last ganglion is connected to the coccygeal nerve by several fine rami communicantes. The ganglia also give off numerous very fine branches, which pass round the dorsal aorta in the form of a very delicate network or **plexus.** A similar but more marked ramification, the **cardiac plexus,** is formed on the surface of the heart, where it is connected with two ganglia to be dealt with shortly, and around the roots of the great vessels. Branches from the third, fourth and fifth ganglia on each side pass ventrally to two large ganglia, the **cœliac ganglia,** situated one on each side of the cœliaco-mesenteric artery, and so form the **solar plexus.** Branches from this plexus run to form marked plexuses of fibres in the walls of the stomach and intestine, and others in the uro-genital organs and the remaining viscera. In fact, branches of this group of nerves spread to all parts of the body in which involuntary muscle fibres are present, and to the various viscera not directly under the control of the will, and hence the term the involuntary nervous system is quite applicable.

The first of the two ganglia in the heart referred to above is **Remak's ganglion** lying in the wall of the sinus venosus, and the second is **Bidder's ganglion,** situated in the auricular septum near the

auriculo-ventricular junction. Both ganglia appear to be connected with twigs from the cardiac branch of the vagus nerve, they are also related to the cardiac plexus, and all combine to regulate the speed and strength of the heart beat.

As has been pointed out previously, a nerve fibre can convey an impulse in one direction only, thus the messages pass along the axon away from the cell and in the dendrons towards the cell. The exact nature of nervous impulse is not known, but it is fairly closely allied to an electric current, although its rate of propagation is relatively very slow, being only about 125 metres per second. It has been found by experiment, *e.g.* by cutting the roots of the spinal nerves stimulating the cut ends and noting the results, that the dorsal root is composed almost entirely of **afferent or sensory fibres,** conducting messages towards the spinal cord, while the ventral root, on the other hand, is **efferent,** carrying its messages to the periphery. Efferent nerves are sometimes termed **motor nerves,** but in the strict meaning of the term they are only motor if they pass to muscles and by stimulating them cause their contraction. If they go to a gland their action is probably to cause an increase in glandular activity, and so they may be termed excitatory, and those going to the heart may cause it to beat more rapidly, *i.e.* are acceleratory or produce the reverse effect when they are termed depressor or inhibitory.

Just as the anatomical unit of the entire nervous system is the neuron, so the functional or physiological unit is the combination of such neurons, termed a **reflex arc.** This in its simplest condition may consist of two neurons. Take an example of a spinal reflex, that is, one occurring in the spinal cord. It consists, in the first place, of the sensory epithelium in which the nerve terminates in a series of small sense organs. On the stimulation of these a message passes up the dendron of the afferent nerve to a cell in the dorsal root ganglion, and thence on by the axon into the spinal cord. Here the terminal dendrites come into relation with the dendrons of an efferent ganglion cell situated in the ventral horn of grey matter, and so the message is handed on. It can then be sent out by the axon of the afferent cell through the ventral root to the corresponding muscle. In this way stimulation of the epithelium will bring about the contraction of the muscle related to it without the intervention of the brain. The whole structure is termed a reflex arc, and the action a reflex action. The arc is not always, indeed but rarely, so simple as this, for generally the terminal dendrite of the dorsal root fibre come into relation with the dendrons of a ganglion cell in the dorsal horn of grey matter, and this cell sends out an axon whose dendrite is related to the dendrons of the ventral horn cell.

This intervening link is termed the **connector neuron.** In many cases even more neurons than this are involved, and the reflex involves quite a complex system of neurons and muscles. Examples of these reflexes can readily be shown in a frog whose brain has been destroyed. If such a frog be suspended and a toe pinched, or the toes dipped in weak acid, the foot will be withdrawn. A spot of weak acid placed on the abdomen will be kicked off by the hind foot, and various other similar actions can be brought about, all of them, as we should say, purposeful. It will be seen that in these cases it is not merely the muscle actually touching the skin that is concerned, but the whole of the muscles of the leg and foot related to and bringing about the movement of the part. Reflex action plays a considerable part in the ordinary activity of the higher animals, and the life of the lower animals appears to be almost entirely made up of a large number of these co-ordinated reflexes often of a complex nature.

When the impulse enters the spinal cord by the dorsal root it is not only sent on to the remaining part of the reflex arc, but it is also transmitted to the dendrons of the cells running longitudinally in the spinal cord. These cells, in their turn, hand it on to similar cells and so form a relay path by which the message is conveyed to the brain, where it may produce various results according to the requirements of the animal. In our own case, although many of these reflexes are very powerful, it is possible to override them by an effort of the will. Thus, for example, if we purposely pick up a hot coal we may suppress the reflex to such an extent that we do not drop the coal, but allow it to burn our fingers. One important function of the brain, then, is to receive the stimuli brought in from all parts, and if necessary to correlate and modify the local reflexes in such a manner as to make for the well-being of the animal as a whole, and not merely of its individual parts. The better able an animal is to order its reflexes to meet the demands of its environment in the very widest meaning of the word, the more advantages it possesses over its fellows not so well endowed, and the more highly developed we regard it.

Sense Organs.

The sense organs comprise the organs of smell, sight, touch, taste and hearing. Three of these, the first two and the last, are compact and surrounded by supporting structures known as capsules, and the other two consist of numerous tiny spots scattered over a more or less wide area.

The **olfactory organ,** the organ of smell, is localised in the olfactory capsule, a cartilaginous structure situated at the anterior end of the

skull in front of the cranium. There are two of these sacs side by side, but completely separated from one another in the middle line by the nasal septum. Each consists of a main chamber communicating with the outside by means of the external nares, and with the inside by the internal nares, which open on the roof of the buccal cavity just in front of the vomers. The floor of the main cavity is occupied by a well-marked swelling and two smaller chambers, a lateral and a dorsal, lead off from it. The whole of the inside of the three chambers is lined by a sensory epithelium. Transverse section shows this epithelium to be simple and columnar, and to contain two varieties of cells. The most important are the long narrow sensory cells which are separated and kept in position by more numerous columnar cells. At the free end of the olfactory cell is situated a small tuft of very delicate sensory hairs, and its inner end is continued on as a fine fibre. These fine fibres unite together in bundles to form small nerves, which pass into the olfactory lobes. Thus these cells are to be regarded as peripherally situated neurons whose axons run into the brain and whose dendrons are represented functionally by the small hairs, inasmuch as they receive the impulse and convey it to the cell. An epithelium built up in this way of neurons and supporting cells is sometimes termed a nervous epithelium. Here and there the epithelium dips down to form simple saccular glands, whose business it is to secrete the mucous that keeps the whole interior moist.

The main function of this organ is olfactory, that is, it is concerned with the perception of smells of various sorts. Owing to the fact that it opens internally as well as externally, it is also used for respiration ; to aid in the carrying out of this latter function the external nares are provided with valves that open and close, regulating the intake of air in a way that has already been described.

The organ of sight is the eye, situated in the orbit at the side of the cranium. It is a more or less spherical structure kept in position by means of its nerve and a series of muscles, which also enable it to be turned in different directions at the will of the animal. When removed from the skull, it will be seen that the eyeball, as it is termed, is tough and more flattened on the outer than on the inner side and possesses a sort of stalk, the **optic nerve.** The inner side also is opaque, whilst the outer, exposed between the eyelids, is transparent, allowing certain internal parts, the iris and the pupil, to be seen through it. If cut in half, it will be found to be a hollow structure with a wall composed of three layers. The external protecting and supporting layer is termed the **sclerotic,** and is composed of a tough cartilage which in its transparent outer portion is known as the **cornea.** The sclerotic encloses the whole eyeball as a sort of

optic capsule, save at the point where the optic nerve leaves it, and here it is reflected, getting thinner to form a sheath for the nerve. The exposed surface of the cornea is closely covered by skin, a continuation of the same skin that covers the whole body and forms the eyelids, but in this region it becomes very delicate and transparent, and is termed the **conjunctiva.** The second layer of the eyeball is

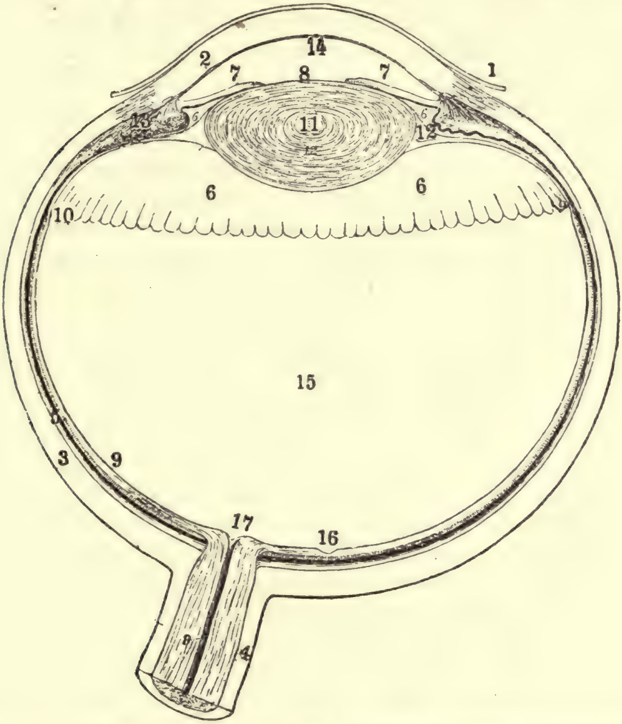


FIG. 31.—View of the human eye, divided horizontally through the middle.—From Furneaux.

1, conjunctiva ; 2, cornea ; 3, sclerotic ; 4, sheath of the optic nerve ; 5, choroid ; 6, ciliary processes ; 7, iris ; 8, pupil ; 9, retina ; 10, anterior limit of the retina ; 11, crystalline lens ; 12, suspensory ligament ; 13, ciliary muscle ; 14, aqueous chamber ; 15, vitreous chamber ; 16, yellow spot ; 17, blind spot.

known as the **choroid coat,** and is formed of densely pigmented connective tissue containing blood-vessels. The choroid layer fits closely on to the sclerotic over the inner parts and, like it, is partly reflected over the optic nerve. At the edge of the cornea the choroid coat leaves the sclerotic and becomes stretched across the eyeball, so dividing it into two parts known as the anterior and posterior chambers. The anterior or outer chamber is filled with a watery

fluid, the **aqueous humour,** while the posterior chamber is filled with a transparent semi-gelatinous mass, the **vitreous humour.** The vitreous humour is bounded by a delicate sheath, the **hyaloid membrane.** The part of the choroid stretched curtainwise across the eye is termed the **iris,** and it is perforated in the middle by an oval aperture, the **pupil.** The iris also is deeply pigmented, appearing bright yellow on the outside, and it acts in the same way as the diaphragm of a camera lens, regulating the amount of light entering through the pupil, which appears as a black spot. In the iris run two sets of involuntary muscle fibres, one set are circular and the other radiating, and so between them they control the size of the pupil. At the line where the iris leaves the sclerotic the choroid coat is thrown into a series of tightly packed radiating folds, well supplied with blood-vessels, the **ciliary processes.** These have unstriped muscles running from their outer edges to the sclerotic cartilage, thus forming a ring of fibres, the **ciliary muscle,** as it is termed. Just behind and touching the iris, and so completely separating the anterior and posterior chambers, is a hard strongly biconvex body, the lens. It is crystalline and quite transparent in the living animal, but becomes opaque after death and is composed of a series of concentric fibres, each derived from a single cell. The lens is held in position by being contained in a thin membranous bag, the **lens capsule,** which is continued out around its circumference into a tough flange, the **suspensory ligament,** in its turn attached to the ciliary processes.

Within the choroid we have the third or internal coat of the eye, the **retina.** This is a neuro-epithelium, and is the part sensitive to light. It lies close to the choroid in the living animal, but is readily detached, save at the point of exit of the optic nerve and when the eye has been cut in half often hangs loosely. The thickness of the retina is approximately the same over the greater part of the posterior chamber, but just behind the ciliary processes it suddenly becomes much thinner, being reduced to a columnar epithelium, and the ridge or step marking the point of this reduction forms a wavy line, the **ora serrata,** running round the inside of the eyeball. The thin part of the retina is continued on over the ciliary processes, where it is termed the **pars ciliaris retinæ,** and beyond this again on to the posterior surface of the iris, but here it is represented only by its pigment layer. The innermost surface of the retina turns in to run through the posterior coats of the eye as the optic nerve, and just at the small point where it does so the retina is not sensitive to light ; thus a "**blind spot**" is produced. At the end of the line passing through the centre of the lens, the optic axis, the retina becomes thinner-forming a tiny saucer-shaped depression, usually having a yellowish tinge, hence termed the yellow spot or **macula lutea,** which is the

point where the perception of the retina is most keen. The blind spot is a little below and behind the yellow spot.

Examined under fairly high magnification a transverse section of the wall of the eyeball shows the sclerotic to be mainly composed of ordinary hyaline cartilage. The choroid is deeply pigmented tissue with a plentiful supply of blood-vessels. The retina exhibits quite a complex structure and its full details are difficult to make out, save in specially prepared and stained sections. When these are employed the full structure can be seen, but even in ordinary sections viewed under comparatively low magnification the relative position of the parts can be easily made out. Under the low power, the retina appears to consist of a series of superimposed layers. Next to the choroid coat is a pigment layer, and then follow in succession layers termed the rod and cone, the outer nuclear, the outer molecular, the inner molecular, the cellular and the fibrous layers. The explanation of this appearance becomes clear when we examine the detailed structure.

The pigment layer is composed of a number of cells, deeply impregnated with pigment, that send processes down between the rods.

The visual sensory cells are the **rods** and **cones.** The rod-cells, which are more numerous than the others, consist of long thread-like cells. Each cell swells out near the inner end to form an enlargement in which the nucleus is situated. These nuclei fall in the outer nuclear layer, the external boundary of which is marked by a thin transparent homogeneous membrane, the outer limiting membrane. Outside this membrane each rod-cell exhibits a spindle-shaped enlargement and then becomes a narrow cylindrical rod, from which the cell is named, both of these parts coming within the designation of rods and cones. The thread-like portion of the cell, passing inwards from the nucleus, terminates in a small knob-like swelling. The whole structure represents a much modified sensory epithelial cell, the rod-like portion corresponding to the dendron, and the knob-like enlargement the dendrite at the end of its axon. The cone-cell has a very similar structure, the principal difference being that the spindle-shaped swelling of the dendron is larger and more marked, and passes on into a very short pointed rod, hence appearing cone-like.

Next come a series of connecting elements in the form of more special nerve cells, whose bodies with their nuclei constitute the inner nuclear layer. The dendron of each cell passes out and arborises round the knobs of the rod and cone cells, thus giving rise to the outer * molecular layer. The axon with a large dendrite comes in the inner * molecular layer, where it comes into functional

* Aborisations of other cells, that have been omitted for the sake of simplicity, are concerned in the formation of these two molecular layers.

connection with the dendrons of the last layer of cells, the transmitting cells. The bodies of these transmitting elements, which are relatively large, form the layer of nerve cells and their axons, the innermost layer, that of the nerve fibres. These pass out, via the blind spot and are continued on outside the eye as the optic nerve into the brain. On the internal surface of the nerve fibres is another thin inner limiting membrane. Between the inner and outer limiting membrane stretch certain non-nervous supporting cells, known as **Muller's fibres,** that form a sort of scaffolding and whose nuclei fall in the inner nuclear layer.

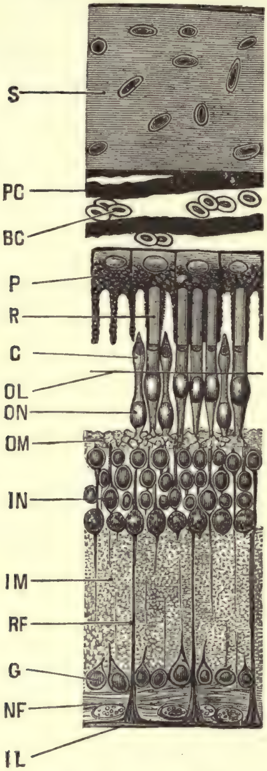


FIG. 32.—Vertical section through the posterior wall of the eye of a frog; the section passes through the sclerotic, the choroid, and the entire thickness of the retina. × 300. — From Marshall and Gamble.

B.C., red blood corpuscle; C., cone; G., ganglion cell; I.L., inner limiting membrane; I.M., inner molecular layer; I.N., inner nuclear layer; N.F., layer of nerve fibres; O.L., outer limiting membrane; O.M., outer molecular layer; O.N., outer nuclear layer; P., pigment cell of retina; P.C., pigment of choroid; R., rod; R.F., radial or Muller's fibre; S., the cartilaginous sclerotic.

The rods and cones are the actual receptive elements in the eye, and it is interesting to note that they are on the outside of the retina, so that the light has to pass through all the other layers before reaching them, after doing which it is stopped by the pigment cells. From the evidence afforded by diseases of the eye, it seems probable that the cones are more particularly concerned with the perception of colour and the rods with variations of light intensity. The whole eye forms a kind of photographic camera, and the amount of light let in is regulated by the iris, which therefore plays the part of the diaphragm. By means of the lens an image of what the animal wishes to see is focussed upon the retina, with the central part of the picture falling upon the yellow spot. As the things looked at are at different distances from the eye, it is necessary that the lens should be capable of forming clear images of both near and distant objects. The distance between the lens and the plate (*i.e.* the retina) cannot be altered as in a camera, but in order to produce the same result the actual shape of the lens itself is altered; it is more flattened

for distant view and more convex for things close at hand. This alteration, termed **accommodation,** is brought about by means of the ciliary muscles. Under normal conditions the suspensory ligament is pulled tight, and so the lens is compressed by its capsule. When a near object is examined the ciliary muscles contract, so pulling the choroid forward, thereby relaxing the ligament and allowing the lens by its own elasticity to assume a more curved shape. When the image, which is inverted, falls on the retina it is, as it were, analysed by the rods and cones and then transmitted to the brain, by the relays already noted, and there it is interpreted. With the advance of age in ourselves, there is usually a gradual increase in the rigidity of the lens, and consequently it becomes harder to see things close at hand, so that glasses have to be worn when reading, etc.

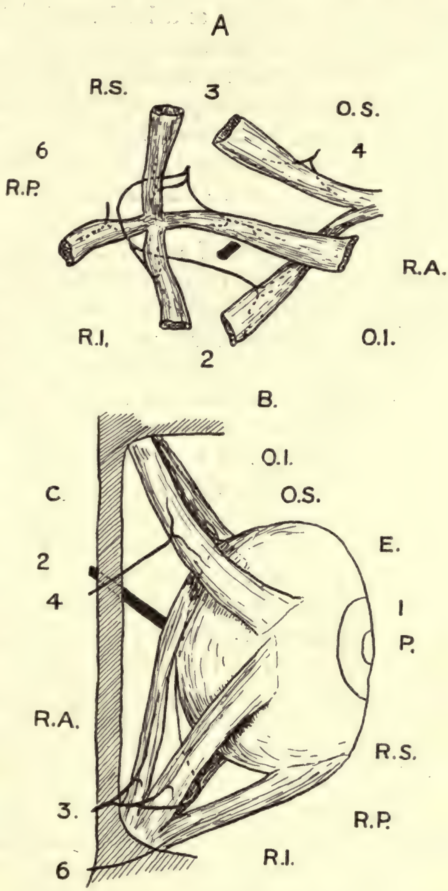


FIG. 33.—Diagram of the muscles of the eye of a vertebrate, *Scyllium.*

A, eyeball removed, viewed from side; B, viewed from above; C., cranial wall; E., eyeball; I., iris; O.T., inferior oblique; O.S., superior oblique; P., pupil; R.A., anterior or internal rectus; R.I., inferior rectus; R.P., posterior or external rectus; R.S., superior rectus; 3, 4, and 6, third, fourth, and sixth cranial nerves.

In order to point the eye in the right direction, it is provided with a series of muscles which are arranged in two groups. The first is a group of four muscles, arising close together at the inner posterior angle of the orbit and inserted on the top, bottom, inner and outer sides of the eyeball. They are termed collectively the recti muscles, and individually the **Rectus superior, Rectus inferior, Rectus internus or anterior** and **Rectus externus or posterior** respectively.

The second is a pair of muscles arising together from the inner anterior corner of the orbit. One, the **Obliquus superior,** runs obliquely upwards and backwards, and the other, the **Obliquus inferior,** runs obliquely downwards and backwards to be inserted on the eyeball. Between them these six muscles, which are to be found in all vertebrate animals, can move the eye in any direction that the animal wishes. The nerve supply of these muscles, which is also constant in vertebrates, has already been indicated.* In the frog there is an additional muscle present, called the **Retractor bulbi,** which surrounds the optic nerve and enables the whole eyeball to be drawn back somewhat into the orbit.

The senses of touch and taste are served by cells which, unlike those of the other three senses, are not aggregated together to form fairly large well-defined sense organs, but are scattered singly or in small groups over a more or less wide area. Touch is located partly in the epidermis, in which nerve fibres form a fine network with ends situated between the cells, and for the most part in the dermis. The tactile and organs of the dermis comprise corpuscles of various sorts, but each consists essentially of a much modified cell or cells, in close relation to which a nerve fibre breaks up into a fine meshwork of arborisations. By means of these different organs the various stimuli that constitute "touch," *i.e.* pressure, warmth, cold and pain, are received and conveyed to the brain. It will be noted that the stimulus only reaches them in a reduced form through the epidermis, with the result that when an accident removes a portion of our epidermis all the stimuli, including pain, appear much magnified when anything is touched by the injured spot. The gustatory end organs subserving taste are naturally limited to the tongue and mucous membrane of the mouth and pharynx. Generally they consist of a group of modified columnar cells, some of which give off branching processes that are related to the ends of the nerves of the plexus underlying the epidermis. The sense of taste is resolvable into at any rate four primary components : Sweetness, Bitterness, Acidity and Salinity.

The auditory organ or organ of hearing in the frog consists of two separate parts, known respectively as the inner ear and the middle ear ; the former is the essential organ of hearing, while the latter is concerned with receiving sound waves and conveying them to the inner ear. The inner ear is constituted by a somewhat complex structure known as the **membranous labyrinth**, and this is lodged in the otic capsule. The labyrinth consists of a membranous sac, **the vestibule,** divided into two parts. The upper larger portion

* The muscles of the vertebrate eye can be studied more readily in *Scyllium*, on account of its size.

is known as the **utriculus,** and the lower smaller one is termed the **sacculus.** Connected with the utriculus are three hoop-shaped membranous tubes, the **semicircular canals.** The anterior of these lies in a plane practically parallel with the sagittal plane of the head, and its lower front end dilates just as it is joining the utriculus to form an **ampulla.** The posterior semicircular canal lies in a transverse plane almost at right angles to the former and, like it, is dilated into an ampulla at its lower end. The upper extremities of both these vertical canals join together to form a common tube opening into the utriculus. The third or horizontal semicircular canal is in a plane roughly at right angles to the planes of the other two, and has an ampulla at its anterior end. From the sacculus arises a small sac-like outgrowth, the **lagena,** which in higher vertebrates is transformed into a very complex spiral structure, the **cochlea,** and even in the frog indications of the beginning of this specialisation are to be seen. The utriculus also gives rise to a small tube, the **ductus endolymphaticus,** which enters the cranial cavity and there unites with its fellow to form a sac, the **saccus endolymphaticus,** filled by a whitish fluid which owes its colour to the presence of very small crystals of Calcium carbonate. A median prolongation from the saccus runs back along the dorsal side of the spinal cord, giving off paired outgrowths which pass out through the intervertebral foramina and form the so-called **calcareous bodies** or **periganglionic glands,** visible as white masses on each side of the vertebral column.

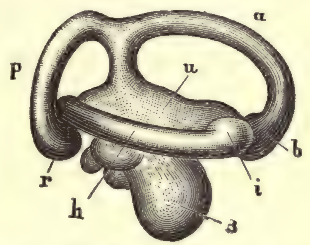


FIG. 34.—The right internal ear of the frog, removed from the periotic cartilage and drawn from the outer surface.—From Marshall and Gamble.

a., the anterior vertical semicircular canal; *b.*, its ampulla; *h.*, the horizontal canal; *i.*, its ampulla; *p.*, the posterior vertical canal; *r.*, its ampulla; *s.*, the sacculus; *u.*, the utriculus.

The whole membranous labyrinth is filled with a fluid, the **endolymph,** and is closely invested by cartilage and bone; the small space left between the labyrinth and the surrounding tissues being filled with another fluid, the **perilymph.** The endolymph contains a number of calcareous granules, the otoliths, which play a considerable part in the functioning of the ear.

The labyrinth is lined by an ectodermal epithelium whose cells are differentiated to form sensory patches here and there. The patches contain pear-shaped sensory cells, each bearing a fine hair-like process with long columnar supporting cells running between them. They may be arranged in small ridges or **cristæ acusticæ,** or

take the form of spots or **maculæ**. Each ampulla possesses a well-marked crista, while the maculæ acusticæ may occur in the utriculus, sacculus or lagena, in which last part there is a spiral band of sensory cells. Branches of the eighth or auditory nerve are distributed to all these sensory areas.

The cavity of the middle ear or **tympanic cavity** is a hollow at the outer side of the auditory capsule, separated from the outside by the tightly stretched **tympanum,** which is supported by a cartilaginous ring, the **annulus tympanicus.** To the tympanum is attached a bony rod with cartilaginous ends, the columella auris, which passes inwards across the roof of the tympanic cavity. The otic capsule is pierced by a small aperture, the **fenestra ovalis,** which would put the perilymph space in communication with the cavity if it were not closed by a cartilaginous disc, the **stapes,** on to which the columella fits. Ventrally, the ear cavity is in communication with the back of the buccal cavity, as we have already seen, by means of the Eustachian tube. In this way the pressure on the two sides of the tympanum is kept the same, and so instead of being bulged either in or out with variations in pressure on the two sides it is kept flat and taut. When sound waves strike the tympanum they cause it to vibrate, and this vibration is given to the columella, which in its turn passes it on to the stapes, thence it travels to the perilymph and so finally to the endolymph, which provides the actual stimulus for the sensory cells.

The function of the ear is twofold. The more obvious is, that it is the organ of hearing, the other function, which although not so obvious is nevertheless the more primitive, is equilibration. The ear of the lower vertebrates is mainly an organ concerned with the balance of the body, and in some cases it is doubtful whether the animals can hear at all, as we understand the term. As we pass up to the higher animals the sense of hearing becomes more and more important, and we lose sight of the primitive function until something occurs that throws it out of gear. The semicircular canals are mainly concerned with equilibration, while the higher developments of the sense of hearing are dependent on the cochlea.

In the nose, the eye and the ear we have had examples of three sense organs, and in spite of their obvious differences we can find certain underlying features that are common to them all. Each of them is connected to the brain by means of its own special nerve, each is lined by an epithelium containing more or less highly modified sensory cells, and this epithelium, as we shall see later, is derived directly or indirectly from the ectoderm of the embryo. These constitute what are termed the **essential parts** of the organ, but in addition we always find a number of other structures, the **accessory**

structures, which support and nourish and, although they are not absolutely essential for the organ to do its work, enable it to function far more efficiently. These accessory parts may be derived from the ectoderm also, as is the lens of the eye, but more often from another and deeper lying set of cells, the mesoderm.

This then completes an outline of the main structure and functions of the nervous system and the sense organs. In the latter we have highly specialised structures for the reception of impulses or stimuli from the outside world, which can straightway send on the messages to the brain. This wonderful organ forms, in the first place, a great co-ordinating centre, in which all these messages, not only from without but also from within, can be received, appreciated, and brought into relation with one another. It further forms a place in which messages can be originated and sent, via the nerves, to any part of the body. Like any other part of the body, the nervous system obtains the energy to carry on its work from the oxidation of its own substance, and this consequently implies the formation of waste substances. This wastage has to be made good by nutriment, or the whole organisation would break down. Local reflexes play some part in the lives of all animals, but in general in complex animals like vertebrates any ordinary stimulus needs more than just a local response ; it needs a reply from the animal as a whole, and the co-ordination of the various actions necessary to produce this result is brought about by the brain. These replies are perceived in ourselves, because they are nearly all conscious replies, but in addition to this, the brain is, in a way not noticed by ourselves, or, as we say, subconsciously, controlling the various organs of the body, accelerating or retarding their action to meet the varying needs of life. It will readily be understood that an organ with such an important part as the regulator, controller and co-ordinator of the other organs of the body, is of sufficient interest to merit a branch of study all to itself. This study of the function of the brain with all that it implies —will, memory, perception, consciousness, and so on—is termed Psychology, and is, save in a very general and vague way, outside the scope of this work.

Ductless Glands.

The organs included under the present heading do not compose a system, as do those treated of in the immediately preceding pages, for they are isolated structurally and functionally independently, but they all have the one prominent feature in common that has given them their name. Like all glands, they contain epithelial cells, but unlike other glands, in which the secretion is poured, either on to a free surface or else into an alveolus, whence it is carried

away by ducts, these structures do not possess a free surface nor a duct to convey off the secretion. They are so obviously glandular in structure that their activity has been generally assumed, and as they are plentifully supplied with blood-vessels, it was also assumed that their secretion must be passed directly into the blood stream, and in consequence it is often termed an Internal Secretion. Although they have long been known, it is only comparatively recently that the great importance of some of these organs has been realised, and even now their functions in some cases have not been definitely ascertained. Some are concerned with keeping the blood in proper condition, and these are termed the lymphoid " glands." Although perhaps it is better not to call these glands at all, since they do not form a secretion, they are included here for convenience. The others, true glands, by means of their internal secretions, which contain one or more enzymes, termed hormones, have a far-reaching effect on the metabolism of the body as a whole, or upon certain parts.

Spleen.

This is a small dark red almost spherical body, situated in the mesentery close to the anterior end of the rectum. Inside its peritoneal covering is a connective tissue capsule, and within this again a framework of connective tissue, in which is contained a large number of closely packed cells of various kinds, forming the splenic pulp. Some of the cells are red corpuscles and different varieties of leucocytes. It is a lymphoid gland, generally considered to be a centre in which leucocytes and probably red corpuscles are produced, and it also serves as a station for the destruction of worn-out corpuscles and the removal of pigment and other waste matters from the blood. Other small lymphoid glands, probably with similar functions, are to be found. In ourselves one pair form the tonsils.

Thymus Gland.

A small reddish coloured oval body about 2 mm. in length is to be found just behind the annulus tympanicus and beneath the depressor muscle of the mandible, this is the thymus gland. It is derived from the dorsal side of the gill clefts of the embryo, and histologically appears much like a lymphoid gland. In the adult it forms a centre for lymphocyte formation, but in the very young animal it appears to play a considerable part in the processes of nutrition.

Thyroid Gland.

This is a small compact oval mass lying just outside the anterior end of the posterior cornu of the hyoid plate. It consists

of a number of small closed vesicles filled with fluid, whose walls are composed of a single layer of cubical epithelial cells. Between these vesicles is a fibrous connective tissue framework with a rich vascular supply. It arises from the floor of the pharynx of the embryo. The secretion of this gland appears to be a protein substance rich in iodine (Iodothyrin), and it exerts an influence over the metabolism of the body. In man a certain disease of this organ leading to its enormous enlargement is known as goitre. Inefficient thyroid functioning in the young leads to a condition known as cretinism, in which both bodily and mental activities are severely upset, giving rise to a state of arrested growth and defective mental development. In the adult a condition, known as myxœdema, ensues when the thyroid fails to perform its function—the hair falls out, the skin becomes puffy, and there is considerable mental deterioration. A marked alleviation of these symptoms occurs if the patient is fed with animal thyroids or injected with an extract of the gland. Thus in some way or other the secretion of the thyroid gland profoundly affects the metabolism of the body, presumable hindering katabolism, and so stopping the normal growth or activities of its parts.

Certain other small glandular nodules, termed the Accessory thyroids and Parathyroids, are also present.

Supra-Renal or Adrenal Bodies.

The position of these glands on the ventral surface of the kidneys has already been pointed out. In the higher vertebrates they are solid bodies composed of two layers, an outer or cortical layer and an inner or medullary layer, and the cells composing these layers are quite different. Both kinds of cells are to be found in the frog, but they are more or less intermingled and without any definite arrangement. The cortical cells are arranged in groups or columns of various sizes, and the cells themselves are of an epithelial character with large spherical nuclei. The medullary cells, on the other hand, do not appear in such definite columns, have smaller nuclei, are more granular, and are of the type termed chromophil cells. The internal secretion of the supra-renal bodies has been isolated, and from it a white powder termed adrenalin can be obtained. When a solution of this is injected into the blood stream it brings about a contraction of the non-striate muscles in their walls, and so causes a great rise in the blood pressure and at the same time gives tone to muscles as a whole. The secretion normally is considered to maintain the tone of the body, and one of the most marked symptoms of Addison's disease, a malady of these glands, is a loss of this tone.

Pituitary Body.

The hypophysis cerebri or pituitary body is, as we have seen, a saccular structure situated at the base of the brain inside the cranium. It is complex developmentally and histologically, but includes a glandular portion of typical epithelial cells, whose internal secretion influences the growth of the body. Disease of the pituitary body leads to a very characteristic condition, known as Acromegaly or gigantism—the hands, feet, jaw and bony parts of the body become much enlarged and exaggerated. The disease does not at first lead to the destruction of the gland, but on the contrary to an increase in size and activity, so that the secretion appears to control or augment growth, particularly that of bone.

In addition to the above glands there are to be found included in other organs of the body patches of cells with a glandular appearance, which presumably produce hormones. Beyond noting the fact that in the case of the reproductive organs the secretions are probably responsible for the development of some of the secondary sexual characters, *i.e.* characters which are not concerned with the actual production or transmission of the sexual products, but nevertheless differentiate the sexes one from the other, it is not intended to enter into any further details of such glands here.

We have already seen that the central nervous system takes its place as the great controlling and guiding centre of the animal, but its action is not all powerful, and it is naturally dependent on the body of which it forms a part. The maintenance of the general normal activities of the body and of the fitness of the whole depend to no small extent on hormones secreted by the ductless glands.

Life History of the Frog.

Early in the year, about the middle or end of March, the frogs awake from their hibernation and seek water, where they congregate in pairs, and the male, almost silent during the remainder of the year, commences to croak vigorously. Reproduction in the frog is sexual, that is, it involves the union of an ovum produced by an adult female and a spermatozoon, the product of an adult male. The male seeks the female and clasps her tightly round the body with his fore limbs, the callous pad on the first finger having become enlarged and roughened to allow of his doing this easily, and they remain together during the egg laying. As the eggs pass from the oviducts to the cloaca and so to the outside the male pours over them the spermatic fluid containing the spermatozoa, and they are fertilised outside the body of the female. The ovum is a single cell with a nucleus, but is very much enlarged by the inclusion of an

enormous amount of food material, the **yolk,** in the form of small spheres. It is half black and half white, the upper, dark, or animal pole contains the nucleus with a certain amount of accompanying cytoplasm, the white or vegetative pole a much greater proportion of inert yolk. The egg when it leaves the ovary is enclosed in a very thin almost structureless membrane, the **vitelline membrane,** and as it passes down the oviduct it has added to this a thicker but still relatively thin coat of a mucilaginous substance. The semen or spermatic fluid contains in addition to albuminous substances a countless number of microscopical cells, the sperms. They are also single cells, and consist of a **head** of denser material, containing the nucleus and a fine thread-like **tail,** by means of which they are able to swim actively for a short time. When they come into contact with an ovum they start swimming vigorously into it until one penetrates the vitelline membrane, which then becomes impermeable to any more. Once inside the membrane the nucleus from the head enlarges and travels towards the nucleus of the ovum, and then the two nuclei fuse together, this actually constituting **fertilisation.** There is produced as the result of this process a large cell with but a single nucleus, formed by the union of the male and female **pro-nuclei,** as they are termed, and this constitutes the fertilised ovum or **oospore,** the germ from which the new being will arise. It is only after fertilisation that the egg can grow up into a frog, so that we are here dealing with an extremely important phenomenon, and it is also a significant fact that the product of fertilisation is a single cell with a single nucleus. The importance of these things leads to their frequent discussion and the use of a special terminology. When we wish to speak of either a male or female reproductive organ without discriminating between the sexes we use the term **gonad,** and in the same way either ovum or sperm can be called a **gamete.** The union of two gametes, *i.e.* fertilisation, produces a **zygote.**

The egg when laid has a diameter of about 1·75 mm. Immediately after impregnation the mucous coat absorbs water and starts to swell up rapidly, until it forms a relatively large transparent sphere, in which lies the black and white fertilised ovum. Hundreds of eggs are laid at the same time, and when they all swell they adhere together to form the large frothy masses common in our ponds and ditches in early spring, and known as frog's spawn.

Soon after the above processes have taken place a groove appears on the animal pole of the egg, and this spreads until it has encircled the whole ovum. Examination of sections shows that this groove passes right through the egg, and that the original nucleus has divided into two, one in each half, so that we now have two cells instead of one. No sooner is this completed than another furrow at right angles

to the first starts, and in a similar way cuts the two cells into four. The next furrow is at right angles to both the preceding, and so is equatorial and not longitudinal. It is situated nearer the upper pole, and consequently divides the egg into four smaller and four larger cells. This process of dividing up, termed **segmentation,** goes on fairly rapidly but less regularly, and as a result there is produced a mass of cells very small at the animal pole and larger at the vegetative pole. Sections show that the ovum is now hollow inside, the cells being arranged around an excentric space known as the **segmentation cavity** or **blastocoel,** and the whole structure is termed a **blastula.** The further details of these changes will be dealt with again later, and only the external alterations noted here. The black

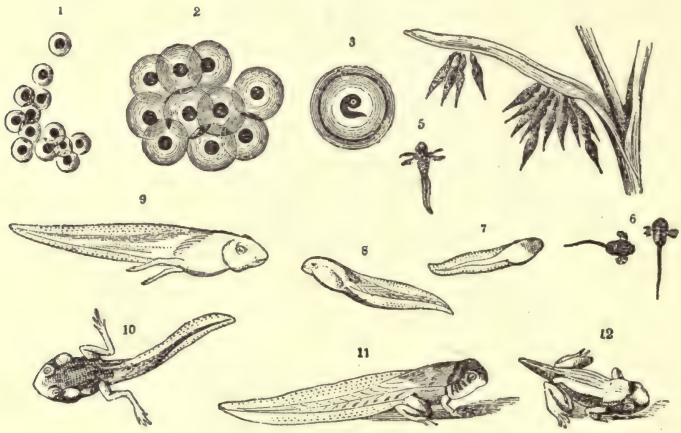


FIG. 35.—The life-history of a frog.—After Brehm.

1–3, developing ova; 4, newly hatched forms hanging to water-weeds; 5, 6, stages with external gills; 7–10, tadpoles during emergence of limbs; 11, tadpoles with both pairs of limbs apparent; 12, metamorphosis to frog.

cells start to grow down over the others, and at about the end of the fourth day the whole egg is black. At the expiration of a week the embryo, as we may now term it, is distinctly oval, and three or four days later a head, body and tail portions are visible. After a fortnight the young animal breaks from the gelatinous envelope and becomes a tadpole. It is now a free swimming comma-like creature with a horseshoe-shaped structure, the sucker, on the ventral surface of the head, by means of which it adheres to weeds or other objects. The food required for its growth so far has been entirely derived from the yolk stored in the egg to start with, and it is not until a few days after hatching that a mouth with horny beak-like jaws develops, and the animal is capable of feeding for itself. As a result of this

feeding the alimentary canal grows rapidly, and is always to be seen through the semi-transparent abdominal wall as a coiled tube. Two pairs of comb-shaped external gills grow out from the side of the neck to be followed shortly afterwards by a third pair. A fold of skin, termed the **operculum,** starts to grow out from just in front of the gills and then to grow back over them. Between, in front, and behind the external gills slits appear, which lead through into the pharynx, and on their walls the internal gills are developed as a series of folds, and with their coming the external gills gradually get smaller. The operculum grows backwards and its hinder edge fuses with the body wall, until at the end of the fourth week it is completely closed, save for a spout-like opening on the left-hand side, which serves for the egress of the water used in respiration.

Tiny little projections, the limb-buds, appear at the base of the tail during the sixth or seventh week; they grow slowly, until a fortnight or so later they are miniature limbs with joints and digits. The front limbs develop at the same time as the hind ones, but they are hidden by the operculum, and do not appear externally until they are practically fully formed. One of them, the left, protrudes through the spout and the other actually bursts through the operculum itself.

Somewhere about the twelfth week a marked and deep-seated change takes place in the tadpole, which up to now has been in many ways extremely fish-like in its internal anatomy. The casting off of the skin allows the eyes to come to the surface, the horny jaws disappear, and the mouth and tongue increase in size. Lungs develop internally, and for a short time the animal breathes by both gills and lungs, but soon by the latter alone; a change that necessitates a radical alteration in the circulatory system. The limbs become stronger and more useful, and with the disappearance of the tail, which has been gradually getting shorter and shorter, the animal becomes a tiny frog. This last rather quick series of changes, whereby the water-dwelling fish-like tadpole becomes transformed into the lung-breathing land-living frog, is termed the **metamorphosis.** A similar metamorphosis is characteristic of all land-dwelling Amphibia. The remainder of the year is passed in feeding till the winter, when this young animal hibernates. It comes forth the following spring, but it does not breed until a year later. Thus the frog passes through a series of changes in a regular sequence, finally reaching the adult stage, *i.e.* not the stage of full growth, but the stage at which it is able to reproduce, and this development is termed the life-history or life-cycle. As long as the young animal is within the egg envelope and entirely independent of the outer world in the matter of food we term it an **embryo.** When it hatches, however, and lives a perfectly

free life, obtaining its food for itself, but still has not attained the form of the adult, that is while it is still a tadpole, it is called a **larva.** The early history of the frog and the metamorphosis of the larva are of importance, since they provide us with an actual example of an animal changing from a gill-breathing swimming form into a land-dwelling quadruped. This is a change that must have occurred in the past when the fish-like Craniates took the all-important step of forsaking the water for the land, and it proved to be the way to the evolution of the higher craniate forms.

Animals and Plants.

In the frog we have seen and studied in some detail a fairly typical example of a highly organised animal, and the examination of its fundamental activities gives a good general idea of the characteristics of the vital phenomena of an animal. Indeed, more than this, the underlying principles are not merely the property of animal life, but they are exhibited by all living beings, animal and plant. Let us consider briefly these points, which fall into four groups.

Firstly, all the living parts of an organism are composed of a very complex substance, Protoplasm, which is a complicated mixture of compounds termed proteins, themselves complex, together with carbohydrates, fats, inorganic salts and water. Even the lifeless products present, such as the hair, scales or feathers of animals, or the bark of trees, are the results of the activities of this wonderful substance protoplasm. It is, in the higher animals and plants alike, split up into units, the cells, consisting of a protoplasmic body controlled by a denser nucleus and modified in almost every conceivable way to perform different functions. One of the main characteristics of protoplasm is its inherent power of contractility or motility, which enables it to alter its shape and move. This is probably brought about by a molecular rearrangement accompanied by certain chemical changes, and although it is more obvious in animals is nevertheless to be found in plants, and is a fundamental property of all living matter. It is to be noted that the alteration is in shape and not in volume, for the protoplasm increases in one direction and decreases in another.

Secondly, all living beings exhibit **metabolism,** and all that that implies. They have the power of taking in dead or lifeless matter and building it up into protoplasm by means of a series of changes, digestion, absorption and assimilation, all implied in the term **nutrition.** The energy required for carrying out this work is obtained from the breaking down of the protoplasm itself, a process that is dependent upon respiration, the process by which oxygen is supplied to and utilised by the tissues. These processes result in the formation

of various waste products, which have to be removed from the body by excretion. As has been pointed out previously, while the building up processes are in the ascendant the organism increases in size, *i.e.* it exhibits the power of **growth.** Again, all living beings obtain energy from the oxidation of their tissues, and this energy appears in the form of heat motion and electrical changes. These particular alterations are more striking in animals than in plants, but, nevertheless, are common to all living beings, which are therefore capable of bringing about a transformation of energy, a point with which we shall deal more fully later.

Thirdly, plants and animals have the power of replying to messages from their environment. This response to external stimuli is not, as a rule, vague or local, but definite and general, and we say, therefore, that they possess **irritability** or **sensitivity.**

Lastly, we have just seen, in the case of the frog in particular, that all living beings pass through a definite life-cycle. They commence as fertilised ova, or as an actual part of the parent, and go through a certain definite pre-ordained series of changes, as the result of which they become adult. When adult they possess the power of carrying on the race by reproducing their like, and, after a certain period in the possession of this power, long or short, as the case may be, they pass on into old age or **senescence.** They finally die, for death is also an integral part of the life-cycle.

Thus far we have been considering the properties common to living beings, and although we are here concerned with Zoology, it will not be out of place to consider briefly the main differences between animals and plants. The differences between the higher animals, such as the frog, dog, or cat, and the higher plants, such as shrubs and trees, are so great that they are apparent to the most superficial observer, and need not be dealt with here. In the case of the lowest members of both kingdoms, simple animals and simple plants composed in many cases of but a single cell, the differences become less and less obvious. Indeed, we actually find a number of organisms, including, for example, the slime fungi, found growing in tan pits and on decaying wood, are claimed by both zoologist and botanist. It has been proposed to give the name **Protista** to this group of beings, which are a mixture of animal and plant, or live as an animal or plant according to the conditions of their environment. It is probable that all living beings have descended from some such primitive organism possessing the potentiality of becoming either animal or plant, and all exhibiting to some degree the various vital powers we have just discussed.

The most fundamental difference between animals and plants is in the chemical constitution of the protoplasm which, small though

it is, manifests itself in a difference of the chemical activities concerned with nutrition. The typical plants are able to utilise as food Carbon dioxide, Ammonium compounds and Nitrates, all of which are generally diffused over the surface of the globe in the soil or carried about by the air and the water. From these simple substances, with the aid of radiant energy trapped from the sunlight, the plant is able to build up or synthesise its protoplasm, a method of feeding termed **holophytic,** or completely plant-like. The typical animal, on the other hand, is unable to do this, and must have a fairly large proportion of proteins in its food. Such substances are not found distributed generally, but only in other living beings, so that the food of an animal must be living or dead organisms; a mode of feeding termed **holozoic,** or completely animal-like. The plant can be, and usually is, quite stationary, and is generally modified in such a way as to expose the greatest amount of surface to the air and the water in the soil, and at the same time attain stability. To do this the plant has developed a spreading root to pick up the nitrogenous substances, and a trunk, by means of which a number of flat leaves are exposed to the air, from which they obtain Carbon dioxide. The stability is attained in some measure by the spreading of the root, which acts as an anchor, but largely by the development of a strengthening substance, usually Cellulose, or a closely allied carbohydrate compound. Therein lies one of the most striking differences between plant and animal histology, in the plant the cell is practically always enclosed in a moderately thick cellulose wall, while in the animal the cell generally has no cell wall, and cellulose and similar substances are absent from the majority of animals. As the food substances of the plant are already in a diffusable form, there is no need for an elaborate digestive mechanism, but it can at once start to build them up into proteins in most cases by the aid of a green colouring matter, chlorophyll, that is not found in typical animals.

The animal, on the other hand, has to search for food, and so is modified for motility, and, as a rule, possesses locomotor organs and a body adapted for movement. The food, too, generally consists of solid particles, and not liquids or gases, and so a temporary or permanent aperture is present in the form of a mouth or its equivalent. Before the food can be injested it is frequently necessary for it to be caught, killed or broken up, and so we find a whole series of mechanisms, claws, teeth, etc., to serve these ends. Even when the food is acquired it is not in a form in which it can be assimilated, and so a simple or complex digestive system is provided to make it available for the body. With the food a certain amount of indigestible matter, supporting structures, etc., is taken in, and has

to be passed out again through a temporary or permanent aperture for egestion, the anus. To co-ordinate these various parts a central nervous system is developed, and in connection with the movements a series of sense organs, which put the animal into touch with the outside world. Practically all the striking characters of an animal are concerned with the question of food, and its whole structure is a complex combination of parts, enabling it to obtain its food readily. In many cases this main object is modified, and sometimes to a large extent by another aim, and that is to enable the animal itself to escape being utilised as food by another animal. All these structural modifications that are for some useful purpose we term **adaptations.**

One further striking difference between animals and plants remains to be noticed, and that is, their gaseous exchanges with the atmosphere. In the case of all organisms, save certain lowly plants, respiration, *i.e.* the exchange of carbon dioxide for the oxygen of the air occurs, and it is more rapid in animals than in plants. Those plants that possess chlorophyll or an allied substance, in the presence of sunlight, take in from the air carbon dioxide, from which they remove the carbon, setting free the oxygen into the air again. This second exchange, which does not occur in animals, is by far the larger of the two in green plants, and almost completely masks the other.

All the vital manifestations of both animals and plants are in reality manifestations of energy, and so it will be well to return to the second phenomenon characteristic of living beings, and examine quite generally the way in which energy is obtained, stored and transformed by organisms. Two kinds of energy are distinguishable: one is kinetic energy, that is, energy that is manifested in the form of motion, heat, light or chemical or electrical changes; the other, termed potential energy, is energy that is stored up in a quiescent condition, only needing some stimulus to release it and allow it to become transformed into kinetic energy. Potential energy in the living being is stored up in a series of fairly complex chemical compounds. Such energy is stored as the result of a complicated sequence of chemical reactions, which lead to the formation of compounds of higher and higher chemical complexity, until we reach that highly organised substance, or intimate mixture of substances, which we term protoplasm. We use the term **Anabolism** to include all these constructive changes culminating in the building up of protoplasm, and this represents, as it were, the credit side of the account, the storage of energy. On the other side we have the debit account, the expenditure of this reserve in the form of kinetic energy brought about by the breaking down of the

complex chemical substances within the organism, and to this whole destructive series of changes we apply the term **Katabolism.** If we wish to include both sets of reactions, that is, energy-storing and energy-releasing, we apply the word **Metabolism.**

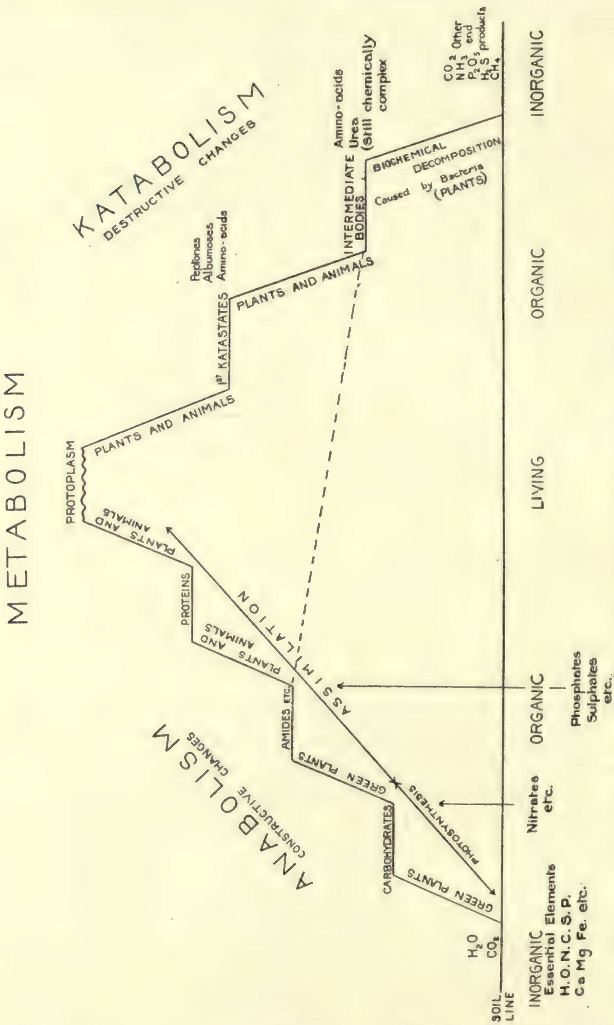


Fig. 36.—A diagram to indicate the various processes concerned in Metabolism. Animals take no part in processes below dotted line.

The first and simplest stages of anabolism are encountered only in the green plant, which is able, as pointed out above, to utilise the radiant energy of sunlight in such a way that from the relatively simple inorganic salts in the soil, or in the air, it can build up com-

pounds known as carbohydrates that are more or less chemically complex, and which we term organic. This power is termed **photosynthesis,** since the building up is dependent on light. Further changes then occur, probably involving the utilisation of energy obtained by the oxidation of previously manufactured organic compounds, and these result in the final production of substances termed proteins, from which protoplasm itself is built, and they are among the most complex bodies known. The typical animal, as we have seen, requires for food organic matter in the form of carbohydrates or proteins. These it breaks up by digestion into somewhat simpler compounds, by means of the chemically active enzymes ; but afterwards, by means of energy obtained by oxidation, it recombines them into proteins and protoplasm. The building up processes in both animals and plants, involving the manipulation of organic compounds and their actual incorporation into the living protoplasm, are distinguished as **assimilation.**

The constitution of living protoplasm is not known with any certainty, since as soon as we start to analyse it we must kill it, and then we have only a mixture of proteins, etc. It may possibly always be a system of such unstable compounds interacting one upon another, and is certainly in a state of continual molecular change, which forms the chemical basis of the vital phenomena, for when they stop life also ceases.

The katabolic or energy-release changes are probably brought about in the main by the action of enzymes, and result in the breaking down of either the carbohydrate food reserves or the proteins, with the consequent production of waste substances, and these reactions are ultimately dependent upon the oxygen obtained by respiration. The dissimilation of the proteins takes place in successive stages, which we may for convenience distinguish as the formation of the first katastates (*i.e.* peptones, albumoses, amino-acids, etc.), and the production of the intermediate bodies like urea, etc.. still moderately complex chemically and still termed organic. These occur in both animals and plants. Just as we find plants at the beginning of the energy-building series, so they come in again at the end, and, as Bacteria, etc., are mainly responsible for the disintegration of the intermediate bodies to form simple inorganic end-products (*e.g.* CO_2, NH_3, P_2O_5, H_2S, CH_4, etc.) ready to be distributed again in the water and air, and serve as food for a new generation of green plants.

This wonderful cycle of metabolic changes is infinitely more complex than has been outlined above, and in spite of the vast amount of work that has been done upon it, many of its details still remain to be discovered. The general idea, however, that underlies it all may be expressed somewhat crudely in a diagramatic manner.

Classification.

The frog, whose anatomy, histology, physiology and, to a lesser extent, development we have now studied, will also serve to introduce another important branch of Biology which follows after these, namely, **Taxonomy** or **Classification.** When we have learned what we can of a new animal it is necessary to give it a name, and to ascertain its position with regard to other animals. The first object, the naming, follows from the second, and cannot be done arbitrarily, for the object of a *natural*, as opposed to an *artificial*, classification is to arrange the animals in groups that show their relationships with one another, and then the name given is one that will indicate the position of the animal in these groups. The theory of descent is the great key to this problem of classification, for it teaches that structural similarity or homology indicates a community of descent, and therefore a degree of affinity, and we utilise this theory to bring animals together in such a way as to make clear their relationships. It is obviously necessary, in order to carry out such a scheme, to have some recognisable unit to form its basis, and so we associate together all animals that possess certain fairly definite and constant characters of structure and form, and this assemblage we call a **species.** This term is hard to define accurately, for it has no absolute criteria or definite limits, but, as ordinarily used, implying a group of beings resembling one another, closely and constantly, and easily recognisable, as belonging to one type, it is a very useful concept, in spite of its vagueness. There is a certain amount of variation within the limits of each species, and each animal has its own individual peculiarities, but they are not so great usually as to obscure the type to which the individual belongs. The constancy that has been referred to is only a relative matter, for although, as far as human remembrance or records go, the species of animals now on the globe are constant, it will be seen that, when we bear in mind the phenomenon of evolution, the constancy is more apparent than real, for they must all have arisen from pre-existing different types. The rate of change, however, is so slow that this alteration is lost sight of. The actual differences separating one species from another are often small, merely differences of colour or size and proportions, as, for example, those between the lion and the tiger, and yet members of one species, as a rule, cannot, or do not, breed with those of another.

When a number of species resemble one another, closely possessing certain characters in common, we associate them together in a larger group that is termed a **Genus.** A species then is a number of individuals possessing in common certain **specific characters,** while genera are groups of one or more species with common **generic characters.** It sometimes happens that a species is so distinct from

other species that none other can be regarded as closely allied to it, and in such cases the genus is composed of that species alone. From these two categories the name of the animal is derived, and a double name results, so that this method of naming is known as the system of **binomial nomenclature.** This system was introduced by the Swedish naturalist, Linne, or Linnæus, in the eighteenth century. It was a great advance on the previous haphazard way of naming, and it is so useful that it is now universally adopted, and, indeed, it is hard to see how the enormous number of species we now know could have been coped with but for its use. The two names are usually of Greek or Latin derivation, sometimes curious mixtures of both, and in some measure correspond to a christian and a surname, save that in the animal the order is reversed, and the generic precedes the specific name.

The name of the common English frog is, as we have seen, *Rana temporaria,* indicating in the first place that it belongs to the genus *Rana.* As pointed out in the opening chapter, another frog, *Rana esculenta,* is common on the continent, and yet another frog, *Rana tigrina,* is common in Northern India. If there is no doubt as to the animal we intend, it is often customary to reduce the generic name to its initial letter, thus our frog becomes *R. temporaria.* These frogs just mentioned are alike in their essential features, and so we find them, with a number of others from various parts of the world, included in the one genus *Rana.* They differ much among themselves in colour, markings and size: the English frog is the smallest, the edible frog a little larger, and the Indian frog considerably larger. It is, therefore, necessary to separate them from one another into separate species, each with its own specific name.

This is a step on the way to classification, but if we stopped here we should still have a large number of genera closely related, or widely separated, from one another, but not in any sort of order. To obviate this we associate allied genera together into **Families ;** these into larger groups termed **Sub-classes** or **Orders ;** these into still larger ones termed **Classes.** The classes that show a certain common fundamental unity of structure, and, therefore, descent from a common, if remote, ancestor, together form a Phylum, one of the major divisions of the animal kingdom.

To take the case of the frog:—

Phylum	Chordata.
Class	Amphibia.
Sub-class or Order	Anura.
Family	Ranidæ.
Genus	Rana.
Species	Temporaria.

The important thing to bear in mind is that too much weight must not be given to the classification of any particular animal, as it merely represents the present state of our knowledge, and if fresh facts come to light might have to be revised. The animal itself is the thing with a real existence, and the various groups, species, genera, etc., are merely convenient abstractions that enable the zoologist to deal with and arrange an enormous mass of material.

Let us now consider the way in which the animal kingdom is classified. It has been noted above that the most primitive animals consist of one cell, and these simple forms are grouped together in the Phylum **Protozoa,** the unicellular animals, and separated from all the remaining forms, which are termed the **Metazoa** or multicellular animals. The Protozoa are not, strictly speaking, unicellular, for although the majority of them consist of only one cell, a large number are composed of many cells joined together. In this case, however, the cells are all more or less similar and co-equal, and they stand in marked contrast to the cells of the Metazoa, which are always differentiated to form tissues. The two groups may be distinguished as cell animals and tissue animals.

The lowest members of the Metazoa are animals composed of two layers of cells: an outer layer, the **ectoderm,** forming the outside covering of the animal; and an inner layer, the **entoderm,** which forms the lining of the one internal cavity of the gut or enteron. They are classified together in the Phylum **Cœlenterata.** The remaining Metazoa have not only the two layers, ectoderm and entoderm, but a third layer of cells, the **mesoderm,** is also present between them. The most typical forms have not only an enteron, but also another cavity situated in, and surrounded by, the mesoderm, termed the **cœlom,** and hence they are distinguished as the **Cœlomata.**

This division, the Cœlomata, is in itself subdivided into two groups: the **Invertebrata** and **Vertebrata,** the former composed of a number of separate Phyla. The term Vertebrata, of course, actually implies that the animal possesses a dorsal column of separate vertebræ, like the frog, and this was how the term was originally employed. It was subsequently found that this segmented vertebral column is always preceded in development by a long unsegmented supporting rod of peculiar structure, called the **Notochord** or **Chorda dorsalis.** Moreover, some of the lower members of the group, *i.e. Amphioxus*, and some of the primitive fishes retain a notochord throughout their entire life, and never reach the stage of development in which it is replaced by segmented vertebræ. The important distinction between the two groups is then the presence of a notochord, and so, strictly speaking, the term **Chordata** should be given to the group and Vertebrata reserved for those members of it with the spinal

column composed of vertebræ. Although this is sometimes done, those animals that never have a notochord are almost invariably classed together as the Invertebrata, and hence, for contrast, some authors retain the term Vertebrata for the remaining group, and include in it all the Chordata. In the widest use of the term Invertebrata it can, of course, include Protozoa and Cœlenterata, but it is convenient to restrict it to invertebrate cœlomates. These two groups differ greatly in relative value, for the Phylum Chordata forms what may be termed a natural group, since all its members are related to one another by community of descent, and all save certain degenerate forms conform to one fundamental plan. The Invertebrata, on the other hand, are simply all the Cœlomates that are not Chordates. It includes various Phyla, each a unit in itself, but not closely or obviously related to one another, and following different plans of organisation. The relations of the main divisions of the animal kingdom, omitting certain small groups, can be expressed schematically as follows :—

- ANIMAL KINGDOM.
  - PROTOZOA.
  - METAZOA.
    - CŒLENTERATA.
    - CŒLOMATA.
      - INVERTEBRATA.
      - CHORDATA (VERTEBRATA).

PHYLA.

Protozoa. *Amœba, Paramœcium, Monocystis, Malaria,* etc.
Cœlenterata. *Hydra, Obelia,* etc.
Platyhelminthes. *Tape-worms,* Liver-flukes, Flat-worms, etc.
Nemertea. Ribbon-worms.
Nemathelminthes. Round-worms.
Annulata. *Lumbricus,* other segmented worms.
Mollusca. Shell-fish, Octopus, etc.
Echinodermata. Star-fish, Sea-urchins, Sea-lilies, Sea-cucumbers, etc.
Arthropoda. Lobsters. Crabs, Spiders, Centipedes, Insects, etc.
Chordata. *Amphioxus,* Sea-squirts, *Scyllium, Rana,* Reptiles, Birds, *Lepus, Canis,* etc.

In the following chapters we shall deal with representative forms from some of these Phyla ; their position in the above table is indicated by the names in italics.

CHAPTER V

THE PROTOZOA

Free-living Protozoa, *Amœba* and *Paramœcium*—Parasitic Protozoa, *Monocystis* and *Plasmodium*.

WE have already seen that the Protozoa comprise the simplest animal forms. In their adult stage they are composed of a single cell with one or more nuclei; or, if of more than one cell, then they form an aggregation of equivalent cells. They are for the most part very small, invisible to the naked eye and requiring a microscope to make them out; but in spite of their small size and simplicity each one is a complete living unit. Each possesses all the characteristics of living matter, and each is capable of exhibiting all the vital phenomena. A certain amount of specialisation within the limits of the cell is nearly always met with, and sometimes quite a number of cell organs are produced each serving some special function. They are widely spread over the whole surface of the globe from the arctic regions to the tropics, in fresh and salt water, as well as in or on the soil, but, as a rule, a fair amount of moisture is necessary for them to keep alive. A very large number of them live on and in other animals, and they bring about a diseased condition in the animal in which they live. Those producing diseases in man are naturally of much importance from the medical point of view. For convenience of study we may divide the Protozoa with which we are immediately concerned into free-living and parasitic forms, although this is by no means a natural classification. To start off with we will take *Amœba*, which is a lowly and little specialised form.

Free-Living Protozoa—i. *Amœba.*

The genus *Amœba* contains a number of species, some even parasitic, and one of the largest and most common is *A. proteus*, the "proteus animalcule" as it was termed by the older naturalists on account of one of its most striking characteristics, that of constantly altering its shape. It is found on the surface of the mud and decaying vegetable matter in ponds and ditches. The animal is

very tiny, one of large size reaching only about 0·25 mm., and so it needs a lens to see it at all.

Under the microscope *Amœba* appears as a mass of fairly transparent granular jelly continually changing in shape by the protrusion of blunt processes, the **pseudopodia,** as they are called. In many ways it recalls the leucocyte of the frog's blood, but it is much larger and more active. Its protoplasm, which is not protected by any form of skeletal structure, is clearly marked off into an outer and an inner portion. The outer layer, the **ectoplasm,** is thin and transparent, and although soft, is firmer than the underlying substance, so forming a protective covering. Inside this, and forming the bulk of the cell, is the **endoplasm,** of a more fluid consistency

FIG. 37.—Different forms assumed by *Amœba proteus*. Photographs from preparations.—From Calkin.

and less transparent, owing to the presence in it of a number of refractive granules. All the vital organs of the cell lie in it, and it flows about freely within the ectoplasm as if confined in a sort of bag. Somewhere near the middle of the cell is the nucleus, a spherical structure not readily seen until the animal is killed and stained. The nucleus is clearly delimited from the remaining endoplasm by a very thin homogeneous membrane, the nuclear membrane. The protoplasm within the membrane is practically indistinguishable from that outside, but contains a large number of minute granules of an important substance termed **chromatin,** because of the readiness with which it takes up certain basic stains. This chromatin, which is in *Amœba* fairly evenly distributed, thus

producing a stippled appearance in the stained nucleus, is a constant and essential constituent of all nuclei in plants and animals alike. The endoplasm also contains certain spaces with a more or less fluid content termed the vacuoles. When the food is taken in it immediately becomes surrounded by fluid, thus constituting a **food vacuole** in which the food is carried freely round in the endoplasm while it gradually becomes digested. Certain other of these spaces appear to contain nothing but a watery fluid, and so are called the **water vacuoles.** Finally, we have a vacuole that is concerned with the elimination of the liquid waste of the body. This may appear quite small, but as we watch it, it gradually gets larger and larger, a process termed **diastole,** until a limit is reached. At this point it suddenly expels its contents to the outside by a sharp contraction known as **systole,** and disappears temporarily to reappear later and repeat the process. From this constant and fairly regular diastole and systole it is known as the **contractile vacuole,** and it discharges its contents through a temporary break in the ectoplasm.

The various granules in the endoplasm are probably minute quantities of digested food on their way to being built up into protoplasm, or stores of reserve material, or particles of protoplasm that are being broken down into waste matter. Collectively they may be called the metaplasmic granules.

When the environmental conditions become unfavourable, *Amœba* assumes a different form. The pseudopodia are withdrawn, the contractile vacuole is often much reduced, and the animal rounds itself off and secretes around itself a tough cyst of chitin or a closely allied substance. Inside the cyst the ectoplasm is more marked than when it is moving about freely. The *Amœba* remains quiescent until upon the restoration of favourable conditions the cyst wall ruptures and the animal comes out again. This encystment is to be regarded as a protective adaptation enabling the animal to tide over periods of stress, etc., and incidentally in this condition it can be more readily conveyed from place to place.

Let us turn now to consider the physiological activities of the *Amœba.* Movement takes place by the formation of pseudopodia, a process that can easily be watched in the living animal. The ectoplasm bulges out to form a small knob, which gets larger and larger, and then all at once the endoplasm bursts into it. This streaming movement may continue until the whole protoplasm has flowed into the pseudopodium, and thus a certain amount of ground has been covered. On the other hand, after pushing out the pseudopodium a short way, it may be withdrawn again. Certain of the different species of *Amœba* can be recognised by the shape of their pseudopodia, which may be single or many, short and blunt,

or long and thread-like. Several pseudopodia may be put simultaneously in *A. proteus*, and so the animal in life presents a very characteristic motile appearance, and, further, its mode of movement is characteristic of a number of other forms of protozoa, and is described as amœboid. Thus *Amœba* exhibits very completely the power of motility.

If we watch a living specimen we shall see that it moves freely from place to place without any apparent cause. This form of movement in ourselves or the higher animals we should term voluntary, but in *Amœba* it is called **automatic** or **spontaneous.** A few simple experiments will show that another sort of movement is also possible. For example, if the slide is jarred, or certain chemicals are added, the animal will withdraw its pseudopodia, or perhaps move away from the chemical, thus acting in response to an external stimulus. Such movements clearly indicating the power of irritability or sensitivity are termed **induced** as opposed to spontaneous. It is, of course, impossible to draw a hard-and-fast distinction between them, for we have no means of knowing what stimuli are playing on the animal, and so we cannot be certain what are spontaneous movements. Some authors go so far as to claim that all movements of *Amœba* can be explained in terms of environmental stimuli. Changes in temperature undoubtedly play a great part in determining the animal's activities, as we can easily test by controlling the temperature carefully. At 25° C. *Amœba* exhibits its greatest activity, and so this is termed the **optimum temperature ;** above and below this it becomes more and more sluggish, movement finally ceasing altogether when the temperature gets very low, near freezing-point, or reaches 35° C. At 40° C. the protoplasm undergoes striking changes and, as we say, coagulates, in the same way as the white of an egg on cooking, and the animal is thereby killed.

Feeding in *Amœba* is a very simple process, the animal flows along until it encounters a particle of food, a piece of organic debris or a diatom, etc. It goes straight on and engulfs or **ingests** the piece which is passed through the ectoplasm into the endoplasm, and there has formed around it a food vacuole. It is necessary that the food should be organic matter of some sort, for *Amœba* is holozoic in its feeding and cannot utilise inorganic substances. Within the food vacuole the organic matter is digested until nothing but an indigestible residue remains. It is not yet possible to examine the substances in the fluid of the vacuoles, although it appears to be acid to start with, and later becomes alkaline. Therefore, by analogy we should expect it to contain enzymes, which are similar in action to those in the digestive juices of the frog, since the composition of the organic food matter is similar in the two animals. When it is

time to get rid of the indigestible residue the *Amœba* simply flows on and leaves the useless particles, termed the fæces, behind, a process known as **egestion** or **defæcation.** Digestion results in the breaking down of the food into comparatively simple substances, and in order that they may be utilised by the cell they have to be assimilated. This assimilation consists of a series of building up processes whereby the simpler compounds are once again transformed into complex protoplasm, and these constructive changes are collectively termed anabolism. Interesting light has been thrown on these processes by a number of experiments in which the *Amœba* was cut into two pieces, one with and one without a nucleus. The part without a nucleus, although capable of living for some days, loses all power of digesting or assimilating food ; therefore, we look to the nucleus as the centre producing the enzymes required for digestion, and as the origin of the chemical activities concerned in assimilation. The digestion of food in *Amœba* takes place in a way markedly different from that in *Rana.* In the latter case the whole of the process is gone through in the alimentary canal, and the food does not pass into the cells of the mucosa until it has been rendered soluble : the digestion takes place in a cavity lined by cells, and is termed **intercellular.** In *Amœba* the raw food is taken straight into the cell within which the digestion occurs, and this in consequence is described as **intracellular**.

There is no special organ in *Amœba* which corresponds functionally to the lungs, but the exchange of Oxygen for Carbon dioxide takes place by diffusion over the general surface of the body. In this way the animal obtains the oxygen required to oxidise its protoplasm and gets rid of the carbon dioxide, one of the waste products resulting from this process.

In order to perform its vital functions it is necessary for *Amœba* to obtain kinetic energy, and this it does by the oxidation of its tissues in the way just indicated. Again, arguing from analogy with the frog, we should expect certain nitrogenous waste matters such as urea to be produced, and these need to be eliminated from the body. It is practically certain that these substances are removed through the agency of the contractile vacuole, and although the amount of fluid it discharges at a time is very small, the presence of uric acid crystals in it has been demonstrated. The vacuole is, therefore, an organ of excretion corresponding in function with the frog's kidney, and, like it, may be concerned with other functions such as the removal of superfluous water, etc.

The phenomenon of growth is clearly exhibited by *Amœba,* and it affords us an interesting example of the way this occurs in living matter. As anabolism proceeds new matter is added throughout

the whole of the cell at the same time, a process of growth known as growth by **intussusception,** which is extremely characteristic of living things, and entirely different from that in inorganic substances. A crystal grows, as noted previously, but only by the deposition of new material on its surface; a method known as **accretion.** Furthermore, a crystal only grows in a solution of the same chemical composition as itself, and it is quite unable to synthesise such a compound from other substances. If any of the digested food remains after the waste of the body has been made good and growth provided for, it is formed into the **reserve material,** scattered as we have already noted in the form of granules throughout the cell.

After a more or less prolonged period of growth the animal reaches its maximum size, and if the food is still plentiful it divides into two by a simple process known as **binary fission.** It is not quite clear exactly what determines the point at which division occurs, but some light is thrown on the matter by a consideration of the relation of *Amœba* to its environment. The respiration of the animal takes place all over the general surface, and so in a small specimen can readily be carried on. As growth proceeds we shall find, as in all solid objects, that while the volume varies as the cube of the diameter the surface only varies as the square. Roughly speaking, then, when the *Amœba* has grown to eight times its original bulk it has only four times its original surface. If we assume that the need for gaseous interchange depends, in the main, on the volume of the protoplasm, then it becomes increasingly difficult to satisfy as the animal grows larger. Division into two cells would, of course, restore the proper ratio again. Other factors, such as the relative size of the nucleus to the cytoplasm and the surface tension of the protoplasm, are also concerned in the process of fission.

The actual process of division in some species of *Amœba* is very simple. The nucleus elongates, becomes dumb-bell shaped, and, finally, divides into two, a good example of direct nuclear division. Closely following this a similar division of the cytoplasm takes place, and so there result two daughter *Amœbæ*.

In *A. proteus* the proceedings are slightly more complex. The chromatin granules in the nucleus become rearranged and take up a median position transversely to the long axis of the elongating nucleus. They then divide up into two groups, one going to each end of the nucleus, so that when the two daughter nuclei are produced each contains a set of granules which are subsequently scattered about as in the original nucleus. This furnishes a very simple example of indirect nuclear division, a process that becomes much more elaborate in the higher animals, and is by far the more common method of nuclear division met with in living beings.

The division of the nucleus is followed by the division of the protoplasm. A somewhat similar process of division occurs in the egg of the frog which divides into two, and each of these again into two, and so on, but here all the cells produced remain together and do not separate as in *Amœba*.

In this production of two new individuals it should be noted that only one parental organism is concerned. There is no question of a

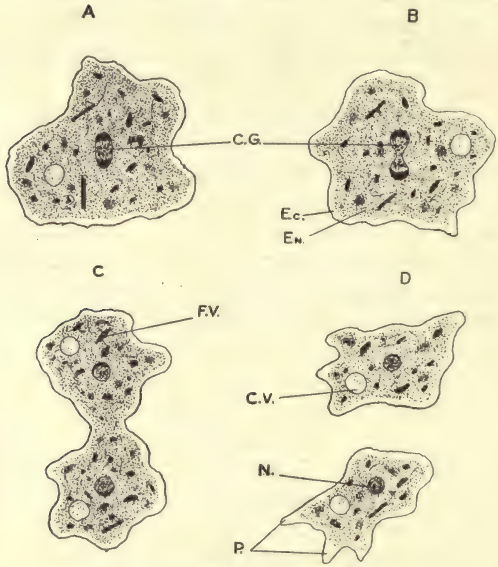


FIG. 38.—Division in *Amœba*.

A, B, C, D, four successive stages in division; C.G., chromatin granules; C.V., contractile vacuole; Ec., ectoplasm; En., endoplasm; F.V., food vacuole; N., daughter nucleus; P., pseudopodia.

male and female parent as in the case of *Rana*, and so we distinguish it as **Asexual Reproduction.**

Another striking contrast with the reproduction in the frog is also presented. When the frog's eggs have been laid and fertilised both the parents remain the same individuals as before. This goes on time after time until death by old age or, much more probably, by mischance intervenes. In *Amœba*, however, the mother organism does not die; it ceases to exist as an individual, but it passes on as two new beings. Hence it is that some writers speak of an *Amœba* as potentially immortal, for we have no evidence to show that it ever dies of old age as do higher forms.

We have seen, then, that *Amœba* is a tiny living unit which, in spite of its small size and great simplicity of structure, exhibits all

the vital phenomena characteristic of all plants and animals, namely, contractility, irritability, metabolism, growth and reproduction.

Free-Living Protozoa—ii. *Paramœcium.*

The genus *Paramœcium*, like the genus *Amœba*, contains a number of separate species of which *P. aurelia* and *P. caudatum* are the commonest, but these only differ from one another in comparatively small points, and a general description will serve equally well for either species. From its somewhat fanciful resemblance to a slipper, the animal receives its popular name of the slipper animalcule. It is to be found plentifully in ponds and ditches, and belongs to that class of the Protozoa known as the Infusoria, from the fact that they appear in infusions of organic matter that are exposed to the air.*

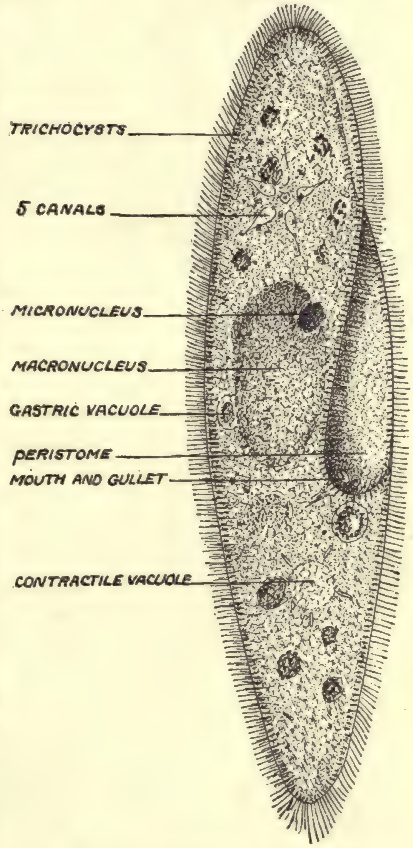


FIG. 39.—Diagram of structures of *Paramœcium caudatum.*

Paramœcium differs considerably from *Amœba* in several important respects: it is larger, reaching a length of 0·3 mm., and so is just visible to the naked eye as a tiny whitish speck; it has a definite shape; it is not a creeping form, but swims about actively, and altogether it is a higher form, having reached a considerable degree of structural complexity. In shape it is somewhat like a cigar, one end is bluntly rounded, and as it lies foremost in locomotion is the anterior end. The opposite or posterior end is more pointed

* A very simple infusion can be made by putting chopped hay into water, bringing it to the boil and then allowing it to cool. If this be placed aside in a cool spot in the open air *Paramœcium* of several species will appear in it after a few days, and subsequently an enormous number will be found.

and is slightly sharper in *P. caudatum* than in *P. aurelia.* An asymmetrical groove, the **peristome groove,** commences as a fairly wide, shallow depression near the anterior end, runs backwards with a slight spiral twist, getting deeper and narrower until about the middle of the body it finally leaves the surface and runs in as a funnel-shaped structure. The hole where the groove leaves the surface is the cell mouth or **cytostome,** and the funnel-shaped continuation, termed the gullet, œsophagus or **cytopharynx,** ends blindly in the endoplasm of the cell. Thus we are able to distinguish not merely anterior and posterior ends, but, the side on which the mouth is situated being ventral, we have dorsal and ventral surfaces, and so also right and left sides. The animal thus has a definite shape which does not change, although it is elastic enough to allow it to squeeze through an aperture slightly smaller than itself, and also to bend round any obstacles that lie in its path. It is enabled to swim comparatively rapidly and uniformly by means of a well-developed locomotor apparatus in the form of a covering of minute motile hair-like processes, the cilia. They are fairly evenly distributed over the whole surface, over the peristome groove, and even in a modified form down the cytopharynx. Owing to the way in which they strike the water and the twist at the front end *Paramœcium* rotates on its own axis as it moves forward much in the same way as a bullet from a rifle or a shell from a gun.

Under the high powers of the microscope further details of its structure can be made out. The protoplasm, like that in *Amœba,* is clearly differentiated into an outer layer, the ectoplasm or **cortex,** strongly marked off from the more granular endoplasm or **medulla**.

The ectoplasm itself is divided into two distinct layers. The outer layer is a thin, tough elastic membrane known as the **cuticle,** formed by the modification of the outer ectoplasm, and giving to the animal its definite shape. The surface of the cuticle exhibits a characteristic sculpturing, being divided up by series of fine grooves into a number of minute hexagons, from the centre of each of which a cilium arises. Each cilium is a minute protrusion of the ectoplasm perforating the cuticle, and it can be traced into its deeper layers where it takes its origin in a tiny speck, the **basal granule**.

The remaining deeper part of the cortex under the cuticle is far thicker and appears transversely striated owing to the presence in it of a large number of very minute spindle-shaped bodies, the **trichocysts,** set at right angles to the surface. Even under the highest powers of the microscope the trichocysts only appear as small simple rods, in which no details of their internal structure can be made out. When the animal is treated with an irritant fluid such as very dilute acetic acid, however, the trichocysts each discharge a very fine

thread, very much longer than the cilia, and so clothe the animal in a matted coating of very fine hairs. The exact use of these trichocysts is almost as hard to understand as their structure is difficult to determine. They are generally thought to be weapons of offence or defence, but have not been observed in use, and are generally only seen when the animal is killed. In the deeper layers of the ectoplasm below the trichocysts are a number of delicate threads disposed parallel to the surface, the **myoneme fibrillæ,** which are highly contractile and bring about the bending movements of the animal. In one species of *Paramœcium,* namely, *P. bursaria,* the ectoplasm contains a number of minute green corpuscles containing chlorophyll, the colouring matter of the leaves of plants, and similar to those we shall describe more fully in the case of *Hydra.* They give the individuals of this species a green colour.

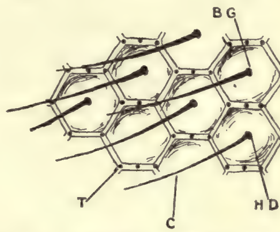


FIG. 40.—Surface view of cuticle of *Paramœcium,* adapted from Bütchli.

B.G., basal granule; C., cilium; H.D., hexagonal depressed area; T., trichocyst.

Two further structures are to be considered as ectoplasmic, although they project deeply into the endoplasm, and these are the **pulsating vacuoles.** They are constant in position, being situated about one-third of the way from each end and, not moving about like the contractile vacuoles in *Amœba,* they discharge always at the same spots. When full they appear as spheres containing a clear fluid, and if they are watched they will be seen to contract suddenly and almost disappear. Careful examination shows that in their place is left a small central spot from which radiate a series of from five to ten fine lines. These lines are the **collecting canals,** and they soon begin to swell up with the accumulation of fluid within them, presenting a very characteristic rosette-like appearance. Finally, they discharge into the central dot, and ultimately they all become merged in the one central vesicle. This process of diastole and systole is continued in a very regular manner as long as the animal lives, and occupies a little less than half a minute. Defæcation in *Paramœcium* always takes place at one spot on the ventral surface, but there does not appear to be any permanent opening. In some forms allied to *Paramœcium, e.g. Nyctotherus,* which lives and is almost always to be found in the frog's rectum, a permanent cell anus or **cytoproct** is present at the hinder end.

The endoplasm differs from the ectoplasm in being far more granular and more fluid, although there is no sharp line of demarcation between the two. The endoplasm is constantly moving round

with a slow circulatory movement termed **cyclosis,** which can readily be seen in the living animal. The granules in it are of several sorts. The reserve food material takes the form of small particles of animal starch or glycogen, and can readily be stained with Iodine which turns them a wine red. Some of the granules of excretory matter appear to take the form of Calcium phosphate. The remaining granules are mostly the indigestible remains of the food. Food vacuoles similar to those in *Amœba* containing a certain amount of fluid and food in a more or less digested state are also present, and render the cyclosis very distinct.

Near the middle of the cell, not far from the cytopharynx, is a fairly large ovoidal body that stains uniformly and very intensely with basic stains. This is the **meganucleus** or **macronucleus,** and near it closer examination will reveal the presence of a much smaller and more lightly staining granule, the **micronucleus.** Thus, unlike *Amœba*, the nuclear matter in *Paramœcium* is contained in two separate nuclei, each with its own particular function.

It has already been noted that *Paramœcium* is a free-swimming animal moving relatively quickly by means of its cilia. As it moves forward it not only rotates on its own axis, but the path it traces is similar to a spiral line drawn on a cylinder. On striking a solid object it is able suddenly to reverse the action of its cilia for a very brief period, and so it recoils a short distance. When it is necessary to change the direction of its course it appears to be able to keep the posterior end relatively still while the anterior end rotates in a small circle. It then moves off at an angle to its former course, and several such movements are required to reverse completely the direction of its progress. As in *Amœba*, its movements may be divided into spontaneous and induced, and, indeed, it shows very marked reactions to mechanical, chemical, thermal and electrical stimuli.

The cilia covering the anterior end are arranged in curved rows pointing into the peristome groove, so that food particles, consisting mainly of bacteria, are gradually driven towards the cytostome. In the cytopharynx the cilia are arranged in a special way. There is a row of long modified cilia partially fused so as to form a ribbon-like structure known as the **undulating membrane.** This, by its wave-like movements, takes the food particles down to the endoplasm where they accumulate in small masses which, when they reach a certain size, become surrounded by a vacuole and pass into the general circulation brought about by the cyclosis of the endoplasm. Within the food vacuole digestion takes place in a manner doubtless similar to that in *Amœba*. A very instructive idea of the part played by the macronucleus in the activities of the cell can be gathered by over-feeding the animal. Under this treatment its

cytoplasm becomes loaded up with dark granules ; in this surfeited condition the animal becomes very sluggish and unable to continue its ordinary activities, and we say it is in a state of depression. If a small quantity of certain Potassium salts be added to the water the dense coloration gradually disappears and normal activities are resumed. It is noteworthy that the protoplasm first starts to get clear in the neighbourhood of the macronucleus, whence it spreads outwards, indicating that this body is the centre of the chemical changes that have taken place in the cell. When all the digestible part of the food has been assimilated the residue is egested via the anal spot towards the posterior end of the animal.

Respiration occurs all over the general surface of the body, and the function of nitrogenous excretion is carried out by the pulsating vacuoles which discharge a fluid containing uric acid in some form ; both are very like the same processes in *Amœba*.

Reproduction is also somewhat similar, and takes place by means of binary fission, the plane of division lying transversely to the long axis of the animal. Just prior to the division of the cytoplasm, division of the nuclei occurs. The meganucleus elongates, becomes dumb-bell shaped, and then separates into two parts, one travelling to each end of the body in a way quite typical of direct nuclear fission. The micronucleus divides slightly later than the meganucleus, and by a form of indirect division. It first enlarges, and the chromatin within it after passing through a reticular or net-like stage breaks up into a large number of definite small rod-shaped bodies known as the **chromosomes,** which pass towards the middle of the nucleus. At each end of the nucleus, by this time somewhat elongated, appears a modified protoplasmic area derived from the division of a sort of nucleolus-like body termed the **nucleo-centrosome.** The areas, from their position at the poles of the nucleus, are called the **polar plates,** and they appear to play an important part in the processes connected with division. Between them appears a number of fine fibrillæ forming the **spindle,** in the

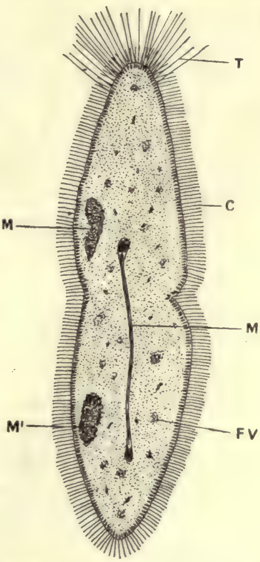


FIG. 41.—Diagram of a longitudinal section of a dividing *Paramœcium*, adapted from a photograph of Calkins.

C., cilia ; F.V., food vacuole ; M. and M[1]., divided macronuclei ; Mi., micronucleus ; T., exploded trichocysts.

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middle of which lie the chromosomes forming the **equatorial plate.** The nucleus now elongates very markedly, and a group of chromosomes pass towards each end. Finally, the nuclear membrane separates, and thus two daughter nuclei are formed which take up positions near their corresponding macronuclei. Shortly after this a circular furrow appears in the central region of the body, and soon we have in the place of the one parent two daughter *Paramœcia.* Each grows until it attains the maximum size, and is then ready to divide.

The process of indirect nuclear division in the micronucleus is more complex than in the nucleus of *Amœba proteus*, and is more advanced in that definite chromosomes, polar plates and a spindle are produced in it, but it must be borne in mind that even here the whole series of changes occurs within the nuclear membrane, a marked difference from the indirect division that we meet in the higher animals, as we shall see later.

The normal method of reproduction, then, is this asexual one by simple fission, a process taking from half an hour to two hours, according to the temperature, and from the one individual a large number are ultimately produced by repeated divisions. It has been found that this process can go on for a long time, and then it gradually slows down and ceases. Change of food will start it off afresh, and an American observer was able to keep the process maintained for nearly two years, during which 742 generations were passed through, but after that no stimulus proved of any avail, and the animals died off. Multiplication by fission can continue for some time, but ultimately a limit is reached, and no change of diet will produce the desired effect, and the *Paramœcia*, unless they are allowed to conjugate, will die out.* The act of **conjugation** appears to bring about a rejuvenescence, and after it, the two individuals concerned serve as the starting points for new series of divisions. If *Paramœcia* be kept in an infusion it will be seen that every now and then nearly all the animals come together in pairs, and what has been termed an epidemic of conjugation sets in. What brings about this impulse to conjugate is not known, but the changes that accompany it have been studied fairly fully. The details vary in different species, but the essential processes are the same, and we will now consider them in *P. caudatum*.

* More recent observations show that a race of *Paramœcia* can be kept going almost indefinitely without conjugation, but in this case the individuals undergo a series of regenerative nuclear changes within themselves. This process of **endomyxis**, as it is termed, is somewhat similar to, and under some conditions can undoubtedly take the place of conjugation. It is to be borne in mind, however, that this occurs under laboratory conditions which are practically inconceivable in the natural surroundings of the animal.

The two individuals that are going to conjugate, and may therefore be termed the **conjugants,** do not differ structurally from other individuals, but perhaps they are slightly smaller. They come together by their oral or ventral surfaces and adhere by their anterior halves. The micronucleus in each enlarges and undergoes indirect division similar to that in binary fission. The daughter nuclei similarly divide so that four micronuclei are produced in each cell, one of which, the one that happens to lie nearest the peristome, persists, while the three remaining ones break up and are gradually absorbed by the cytoplasm. While they are disappearing the remaining micronucleus again divides into two. The one lying

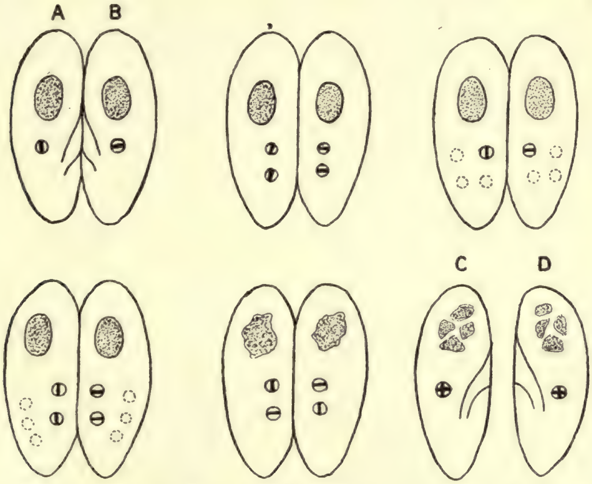


FIG. 42.—Diagram of conjugation in *Paramœcium,* to show the nuclear changes. The position and size of the nuclei are purely diagrammatic.

A. B., conjugants ; C. D., ex-conjugants.

further from the cytostome we distinguish as the **stationary nucleus,** because it remains behind in the cell that produced it. The other, nearer to the cytostome, is the **migratory nucleus,** and is destined very shortly to pass over into the other conjugant. When this happens each individual possesses two micronuclei, one descended from its own original micronucleus and the other that has migrated into it. These two nuclei fuse together and give rise to the **conjugation nucleus,** and then the two conjugants separate from one another. We have thus as the essential part of conjugation the fusion of nuclear material derived from two distinct individuals, and it will be remembered that a somewhat similar fusion is characteristic of the phenomenon known as fertilisation in the Metazoa.

The macronucleus takes no part in these changes at all, but remains unaltered. After the separation, or perhaps before, however, it breaks up into smaller and smaller fragments which are gradually absorbed and play no further part in the activities of the cell.

The mouth which has disappeared in both individuals is now re-formed, and so each **ex-conjugant** consists of a more or less normal free-swimming and feeding *Paramœcium*, save that it only possesses one nucleus, the conjugation nucleus. This nucleus undergoes three successive divisions, giving rise to eight nuclei, four of which migrate to the anterior and four to the posterior end of the animal. Those at the anterior end grow and turn into macronuclei, while of those at the other end, three disappear altogether and the fourth remains as the micronucleus. The ex-conjugant, a form with five nuclei, is now ready to undergo fission, which it soon does if conditions are favourable. The micronucleus divides indirectly and the macronuclei are distributed equally to each daughter individual, thus leaving each with three nuclei. Another similar division follows, so that the ex-conjugant gives rise to four daughter individuals before the ordinary arrangement of one micro- and one macronucleus is restored, and these then serve as starting points for new series of asexual divisions.

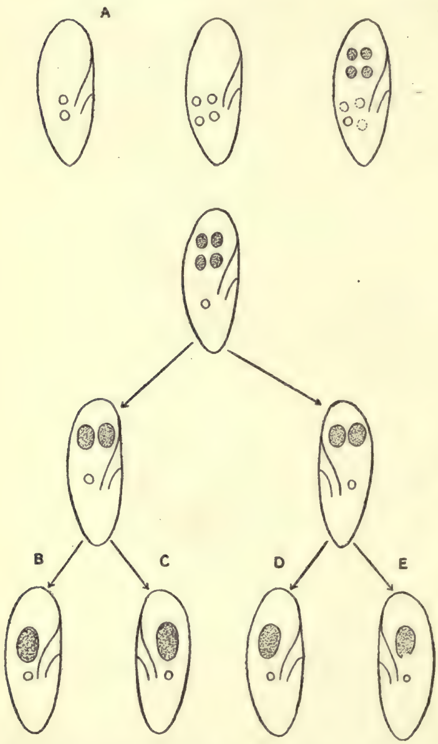


FIG. 43.—Diagram of the nuclear changes leading to the production of four typical *Paramœcia* from an ex-conjugant. The position and relative size of the nuclei are purely diagrammatic.

A., ex-conjugant after the first division of the conjugation nucleus; B.–E., normal *Paramœcia*.

From the description that has just been given it will be seen that conjugation is not strictly speaking a method of reproduction, because

only two individuals result from the union of two. It is, however, closely bound up with multiplication, since two divisions, resulting in the production of four individuals, must necessarily intervene before the typical nuclear arrangement is restored. The main function seems to be a rejuvenating process, so preventing the extinction of the race owing to exhaustion. It differs from sexual reproduction in the higher forms in the absence of the formation of visibly differentiated gametes. A further difference is to be seen in the fact that in the higher animals, after one or a limited number of reproductive periods, the parent forms die. In other words, in the Metazoa the somatic or body tissues are perishable and only the germ cells are potentially immortal. In a similar way *Paramœcium* and *Amœba*, too, for that matter, may be regarded as immortal for, excepting accident or disease, death does not appear to come into the life cycle of these animals.

The conjugation is termed partial because the whole of the two animals does not fuse ; it is merely a fusion of muclear material, and as far as we can see, no fusion of the cytoplasm of the conjugants occurs. The union, too, can hardly be spoken of as fertilisation, as no gametes are produced. The micronuclei are the important factors in the process, and the essential part of conjugation consists in the union of the two nuclei to form the conjugation nucleus.

Although the nuclei play such an important part, the meganucleus is not concerned at all, and disintegrates during the process, thus remotely recalling the fate of the soma or body of the higher animals. The micronucleus is alone concerned, and to distinguish the parts played by the two nuclei the larger is often termed the **tropho-nucleus,** since it is concerned with the feeding or trophic functions, and the smaller, the **gono-nucleus,** since it is related to reproduction. By some authorities they are regarded as one nuclear apparatus in which the **trophochromatin** is separated from the **idiochromatin** or reproductive chromatin, while generally, as in *Amœba*, the two varieties of chromatin are indistinguishably mixed.

Another interesting point is the elimination of a certain amount of nuclear material from the micronucleus in a way that recalls, as we shall see later, the rejection of nuclear matter from the ovum of the Metazoa preparatory to fertilisation.

The two nuclei remaining from the divisions of the original micronucleus do not differ in appearance, but because one of them migrates into the other individual in the way the nucleus of the sperm penetrates the ovum it is sometimes called the male pro-nucleus. In the same way the stationary one is distinguished as the female pro-nucleus. The divisions of the micronuclei are of a

primitive kind of indirect division, but all the changes take place entirely within the persistent nuclear membrane, and no extra nuclear spindle or centrosomes are formed.

If we compare briefly *Amœba* and *Paramœcium* we see that the latter is a more complex animal than the former. In *Amœba* we have a comparatively simple mass of protoplasm, almost an ideal primitive cell, that is capable of exhibiting all the vital phenomena, almost the only specialised part being the contractile vacuole. *Paramœcium*, on the other hand, has a definite protective and supporting cuticle, a locomotor apparatus in the form of cilia, excretory pulsating vacuoles, contractile myoneme fibrillæ, a cytostome, cytopharynx, trichocysts, and so on. All of these are definite structures which can perform special functions that in *Amœba* are carried out by the general protoplasm. Here we have an example of a very important principle underlying animal organisation, namely, the **division of physiological labour,** accompanied by the production of special parts to subserve definite functions, or, as we say, by a **differentiation of structure.** The higher we pass in the scale of animal life the more complete is the division and the more elaborate the specialisation. The frog affords an illustration of this, for not merely are certain parts separated off for set purposes, but the one function itself may be subdivided. Thus the function of digestion carried out in *Amœba* and *Paramœcium* by the food vacuoles, is delegated to the alimentary system in *Rana*, and this in itself is composed of a number of separate organs, each with a limited part to play. One result of this is that the various bodily activities can be carried out with the maximum efficiency. On the other hand, however, when a tissue has become so highly specialised, it can do one thing only and nothing else, so that the maintenance of life depends on the activity of large separate parts. If any one of these ceases to function, life stops, and so we find a number of "vital organs," the elimination of any one of which by accident or disease brings about the death of the whole animal. A comparison is often drawn between this separation of functions in the animal body and the division of an industrial community into different trades and occupations of varying utility to the remainder. The analogy, although not perfect, is fairly close, and here again the complete cessation of work on the part of certain classes of operatives would bring the whole industry to a standstill. This would only be temporary, however, since men are not so highly specialised that they are incapable of doing any other sort of work, and a fresh set of workmen could soon be trained. In the community, as in the animal, increased efficiency is purchased at the price of increased vulnerability.

Parasitic Protozoa.

The two protozoa just considered are free-living forms, that is to say, they move about freely from place to place finding and catching their own food. On the other hand, a large number of the Protozoa do not do this, but live on, and in, other animals whose tissues and juices they use as food. Animals living in this manner are termed **parasites,** and the form upon which they live is called the **host.** One whole class of the Protozoa, namely, the class SPOROZOA, is composed entirely of parasitic species. The Sporozoa possess certain characters in common. They all live inside the bodies of their hosts and so are internal or **endoparasites,** some living in the cavities of the viscera, but others actually inside the individual cells; the latter we distinguish as **intracellular,** and the former as **intercellular parasites.** As a general rule, each species is limited to a definite species of host to which in many, perhaps the majority of cases, they appear to bring no harm, and so are described as harmless parasites. In other cases they are very harmful, setting up a diseased or pathological condition which produces great bodily disturbances, and may even prove fatal. They all live on fluid food which is absorbed by osmosis over the general surface of the body, so that as a result they lack a mouth and a pharynx, either permanent or temporary, also, as it is food already digested and even assimilated by the host, they have no food vacuoles and no contractile vacuoles. There is no need for them to move actively to find nutriment, so that locomotor organs are absent. The name of the class is derived from another of their principal characteristics, and that is that reproduction takes place by the formation of **spores.** In the process of spore formation, or **sporulation,** the parent individual breaks up into a large number of minute nucleated fragments of protoplasm, often protected in some way or other, which serve for the dissemination of the species and the spreading of the parasites to new hosts. Two members of the class we shall now study in some detail, namely, *Monocystis* and *Plasmodium.*

Parasitic Protozoa—i. *Monocystis.*

Two species of *Monocystis,* namely, *M. magna* and *M. agilis,* are to be found in some stage of their life history in practically every ordinary earthworm, and so serve conveniently for purposes of study. They are both to be discovered in the **sperm sacs** of the earthworm, large conspicuous whitish sacs lying in the ninth to twelfth segments of its body, in which the sperms undergo part of their development and are stored until required for use. *M. magna* in the mature condition may reach a length of 5 mm., and so is

visible to the naked eye. It is to be found inside the sperm sacs attached to the rosette-shaped funnels of which there is a pair in segments 10 and 11, and which lead from the sacs to the sperm ducts or vasa deferentia. *M. agilis*, on the other hand, is a far smaller form, only reaching a length of 2 mm. when fully grown. It floats freely in the fluid contents of the sperm sac, and can be found by smearing these on a slide and examining the smear under a microscope. The two species are very similar save in size, and pass through practically similar life histories, so that one description will apply almost equally well to either.

The adult organism is of an elongated spindle shape, somewhat flattened, and contains near the middle a fair-sized nucleus. Its protoplasm is divided into a fairly clear firm ectoplasm, outside which is a very thin but distinct **cuticle** marked with delicate longitudinal striations and a more fluid internal endoplasm. In the deeper layers of the ectoplasm are a number of **myoneme fibrillæ** which branch and anastomose, forming a fine but somewhat feeble contractile network by means of which the movements of the body are brought about. The endoplasm is opaque, owing to the presence in it of a large number of granules of reserve food material composed of a Carbohydrate substance allied to starch. The opacity partly hides the nucleus which, however, cannot even be rendered conspicuous by ordinary stains. The nucleus, which is spherical with a definite nuclear membrane, contains a clear nuclear sap wherein float several deeply staining nuclear corpuscles. These bodies are composed of a basis of a substance **plastin,** impregnated with chromatin, and are termed **karyosomes** in order to distinguish them from true nucleoli, which contain plastin alone. The animal just described is in its feeding or trophic stage, and is in consequence called a **trophozoite.** Its movements are very restricted, it may bend slightly and is only able to move quite slowly. When it progresses a wave of contraction passes from one end of the body to the other, followed by another wave, and so on. This produces a very characteristic form of motion termed **euglenoid** movement, since it is exhibited in a typical manner by the protozoon *Euglena*, one of the MASTIGOPHORA. As has already been pointed out, feeding takes place by osmosis, proteid material, built up by its host, the earthworm, being absorbed from its surroundings. In the same way respiration and nitrogenous excretion occur all over the surface, and no special organs are developed. Reproduction is more complicated than in *Amœba* or *Paramœcium*, and forms parts of a noteworthy cyclical series of changes.

Life History.

When it first reaches the sperm sac, *Monocystis* is a very minute form, and it bores its way into a sperm mother cell becoming an intracellular parasite. The sperm mother cell divides into a number of daughter cells that become arranged to form a mulberry-like mass, the sperm morula, around a central mass of non-nucleated protoplasm, the **cytophore.** The young trophozoite lives in the cytophore, which it gradually consumes. The cells of the morula, after a certain number of divisions, give rise to numerous spermatozoa which assume the typical form with a head and long thread-like tail. By this time the parasite has consumed the central protoplasm, and it now attacks the heads of the sperms, leaving the tails untouched. It is now fairly well grown, and, with all the tails of the spermatozoa adhering to it, looks as if it were covered with a coating of long cilia. For a while it lives in the spermatic fluid, thus becoming an intercellular parasite.

When full grown and mature two of these trophozoites come together lengthwise and adhere. They shorten considerably and secrete around themselves a very tough double-layered spherical **cyst,** composed of a rigid outer coat or **epicyst** and a softer **endocyst.** As these cells are destined to produce the gametes, they may now be spoken of as the gametocytes. The nucleus in each passes through a certain series of changes, resulting in the elimination of a quantity of nuclear substance that is absorbed by the cytoplasm, and then it undergoes repeated division, producing many daughter nuclei. These take up a position around the periphery of the cell, and the superficial cytoplasm breaks up into an equal number of small masses, each enclosing a nucleus and attached to a central lump of residual protoplasm. When they afterwards become free we can distinguish these minute nucleated bodies as the **gametes,** and they soon enter a brief motile stage. The double layer of cuticle that came between the two original gametocytes breaks down and the gametes move about and come together in pairs, the two in each couple most probably being derived from different parents. These pairs and their nuclei fuse to form a single cell, the **zygote** or **sporoblast.** Each zygote secretes around itself a very tough resistant cyst, the **sporocyst,** made of a substance allied to chitin and of a characteristic elongated lemon shape. From its resemblance to one of the unicellular plants, a diatom *Navicella,* in its turn so named from its boat shape, the sporocyst has long been known to naturalists as the **pseudonavicella.** The nucleus of the sporoblast undergoes three successive divisions, giving rise to eight daughter nuclei, which take up a peripheral position near the middle of the length of the

sporocyst. Curved pieces of protoplasm are separated off and enclose each nucleus, leaving a small mass of residual protoplasm. The eight minute bodies so formed are termed the **sporozoites** or **falciform young,** the last name being bestowed on them from their

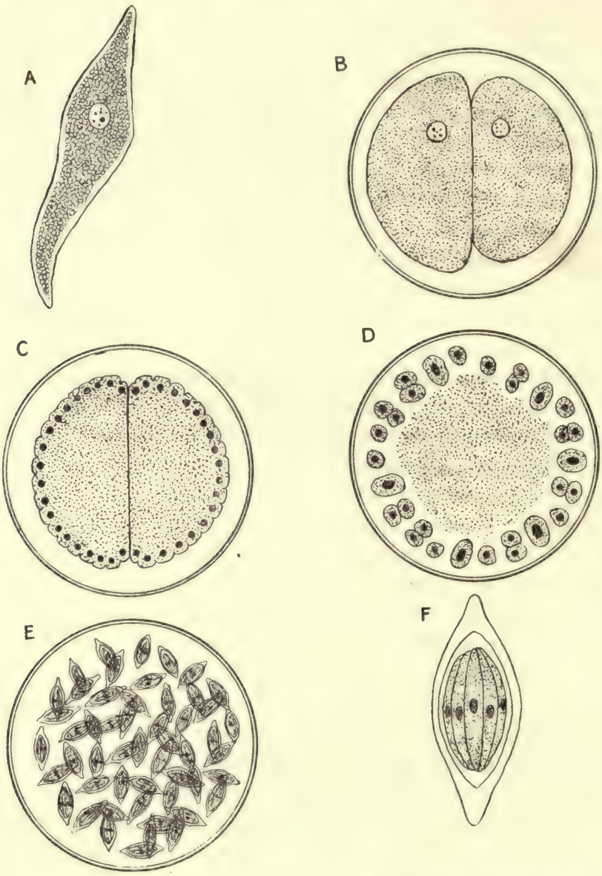


FIG. 44.—Diagram of life history of *Monocystis*, adapted from various authors.

A., trophozoite ; B., two individuals, conjugants or gametocytes, encysted ; C., formation of gametes ; D., union of gametes to form zygotes or sporoblasts ; E., mother cyst with sporocysts ; F., one sporocyst under higher magnification to show sporozoites.

somewhat fanciful resemblance to a sickle blade. Thus we have inside the original mother cyst a large number, at least fifty, and probably many more, of sporocysts, each containing eight sporozoites, and this is the stage most commonly found. No further

development can take place until these sporozoites are transferred to another worm. The eaxct method in which this takes place is not known, but it is plausibly suggested that when the earthworm dies and disintegrates the cysts are left unaffected in the soil; or, again, when a worm-eating bird swallows the earthworm it is able to digest it, but not to injure the resistant spores, which pass through the alimentary canal and are scattered on the ground with the excrement. Another worm swallows the soil containing some of the spores, and so in a chance manner becomes infected. The sporozoites are probably released in the alimentary canal, whose digestive juices are able to dissolve the tough wall of the sporocyst, but it is not yet known how they reach the sperm sacs. Once here they enter the sperm mother cell and the cycle begins all over again.

We see a considerable difference between the method of reproduction in *Monocystis* as compared with either *Amœba* or *Paramœcium*. In the latter two forms the multiplication always takes place by binary fission, *i.e.* division of the nucleus into two, followed by a corresponding splitting of the cytoplasm. The former animal, when it divides either as a sporoblast or as a gametocyte, behaves differently. The nucleus, first by repeated indirect division, gives rise to eight or a large number of daughter nuclei, and not until the nuclear divisions are quite complete and the daughter nuclei have migrated to the periphery does any separation of the cytoplasm occur. Then as many separate small cells as there were nuclei are formed simultaneously. This type of multiplication is distinguished as **multiple fission,** as opposed to binary fission. Another interesting difference is to be found in the life histories, for in *Monocystis* we first encounter in a simple form the phenomenon known as " **alteration of generations** " or **metagenesis.** In the first place we have the sexual generation ending with a large number of gametes which unite to form zygotes, and in the second place the zygotes themselves multiply asexually to produce eight sporozoites. It is to be noted, however, that once the sporozoites have been formed they do not divide any further, as commonly occurs in other allied forms, even when they enter into their feeding stage in the sperm sacs. This particular sort of life history with its alternation is termed **digenetic,** in contradistinction to the simple one in *Amœba,* which is said to be **monogenetic.**

The two gametocytes each produce a large number of gametes which fuse in pairs to form zygotes in a way suggestive of the fertilisation of the ovum by the sperm in the higher animals. The two gametes, however, are, as far as we can see, exactly the same in size and structure, and we cannot distinguish a male and a female form

as in some Sporozoa. For this reason they are termed **Isogametes,** and the process of their union is spoken of as **Isogamy.**

To all appearances *Monocystis* is quite a harmless parasite, and does not seem to have any evil effect upon its host; indeed, it is so widely spread that almost all worms are infected to a greater or less extent. The only parts affected are the sperms, and these are produced in such quantities that even in the case of a heavy infection there are still sufficient healthy sperms to do the work of fertilisation.

Parasitic Protozoa—ii. *Plasmodium,* the Malarial Parasite.

Three species of the genus *Plasmodium,* causing in man three distinct diseases, malaria and two kinds of ague, are known: *P. immaculatum* (or *P. falciparum*), producing pernicious or tropical malaria; *P. vivax,* producing tertian ague; and *P. malariæ,* responsible for quartan ague. The diseases are very widespread over the tropical and temperate parts of the world, and were at one time common in the fenlands and low-lying districts of England, where now, fortunately, they have practically disappeared. Often tracts of country are devastated by their ravages, for they may be deadly, as England found to her cost in the Walcheren expedition in 1809. In this force, out of 39,219 men, 4175 died, the number who suffered from the disease was nearly 27,000, and even when the troops were recalled and reached England, 11,500 were suffering from "Walcheren sickness," as it came to be called. It was long associated with very damp soils, hence its name of marsh-fever, and also the word malaria, *mal'aria,* which means the bad air of marshy places, and which was supposed to be poisonous.

The discovery in 1882 that the disease was caused by minute sporozoa in the red blood corpuscles we owe to A. Laveran, a French military medical officer, and the satisfactory working out of its complex life history may well be regarded as one of the biological triumphs of the end of the nineteenth century. The life history, practically the same in the three species, is more complicated than that of *Monocystis,* since it is intimately connected with two distinct animals, man and a blood-sucking mosquito of the genus *Anopheles.* We term the species in which the sexual part of the life cycle is gone through, in this case the mosquito, the **principal host,** and that in which the asexual period occurs, here a man, the **secondary host.** These two terms, principal and secondary, are applicable generally to the life histories of all parasites, but in the case of malaria and certain other diseases it is often customary, especially in medical works, to entirely reverse the terms. In

dealing with malaria man is termed the principal host, since he suffers a disease, while the mosquito is the secondary host, for the parasite is quite innocuous to it, but this usage of the terms is not strictly biological.

The parasite, when it is introduced into the blood stream of a man by the stab of an infected female mosquito, has the form of an extremely minute spindle-shaped **sporozoite.** The sporozoite immediately attaches itself to a red blood corpuscle, into which it bores its way, and when inside enters into the **trophozoite**, or feeding

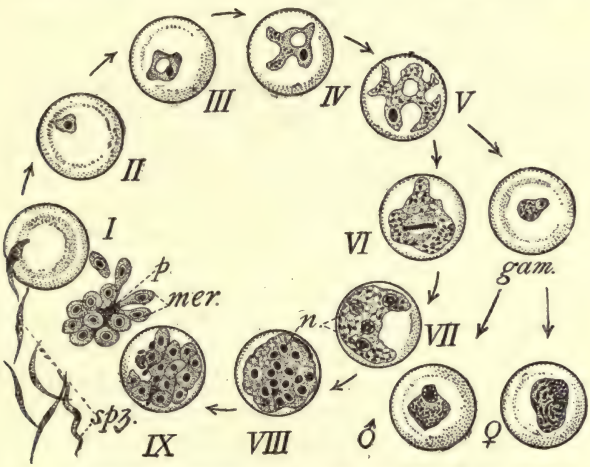


FIG. 45.—A diagram illustrating the stages of the life cycle of *Plasmodium vivax* found in human blood.—From Bourne.

I.-IX. show the schizogonous cycle. In *I.* a sporozoite is boring its way into a red corpuscle; *II.*, young amœboid phase; *III.*, a vacuole has appeared near the nucleus giving the characteristic ring form; *IV.* and *V.*, pigment (melanin) granules are deposited in the cytoplasm, the parasite has increased in size and exhibits active pseudopodial movements; *VI.*, nucleus with an equatorial ring of chromatin granules; *VII.* and *VIII.*, successive stages of nuclear division; *IX.*, segmentation of the cytoplasm round the nuclei to form the merozoites which are shown at *mer* escaping into the blood plasma. *spz.*, sporozoites; *p.*, pigment granules; *gam.*, a young gametocyte; ♂, a male gametocyte (microgametocyte) and ♀ a female gametocyte (macrogametocyte) of *P. xivax*, In this species and in *P. malariæ* the gametocytes are not crescent-shaped as they are in *P. immaculatum.* (Somewhat diagrammatic after Schaudinn.)

stage, assuming an amœboid form. At first very tiny, it gradually grows until it almost fills the corpuscle; it acquires a large vacuole, and granules of a dark pigment termed **melanin** are formed in it. When fully grown the amœboid movements slow down, the vacuole disappears, and the animal rounds itself off preparatory to entering into a reproductive phase. The form of multiplication undergone is termed **Schizogony,** and the individual about to pass through it is consequently known as the **Schizont.** The nucleus divides indirectly a number of times, giving rise to from twelve to sixteen daughter nuclei. As in all multiple fission the cytoplasm next divides into the

same number of separate minute bodies, known as the **merozoites.** These discrete masses are arranged in a radiating manner around a central mass of residual protoplasm, in which all the melanin has accumulated, and so a very characteristic form, known as the " rosette " stage, is entered upon. The corpuscle then breaks down and the merozoites are set free to attack a fresh set of corpuscles, and the melanin is discharged into the blood. The merozoites behave in precisely the same way as the sporozoites, and a fresh cycle is again gone through. In the recurrent forms of the sickness a day of high fever alternates with non-feverish intervals, and it has been shown that this fever corresponds with the end of the schizogonous cycle and the discharge of the fresh lot of merozoites into the blood. In tertian ague (*P. vivax*) this occurs every third day, and in quartan ague (*P. malariæ*) every fourth day. The schizogony in *P. immaculatum* is not so regular, and the merozoites are discharged constantly into the blood, the result being either a continuous fever or one recurring at quite irregular intervals.

It will be seen that if this process goes on an increasing number of red corpuscles are infected and destroyed, and after a comparatively few schizogonous cycles an enormous number will have been attacked even from a small original infection. The patient becomes anæmic, the pigment is deposited in the brain capillaries and certain of the viscera, the spleen becomes enlarged and congested, and general cachexia ensues. This may prove fatal, but if it does the parasites are destroyed with their host and not able to reinfect, so that the death of the host is obviously an undesirable event from the point of view of the parasite. We find generally that after a number of schizogonous cycles have been completed the trophozoite does not turn into a schizont. On the other hand, probably as the result of chemical changes in the blood, it does not reach such a large size, but rounds off slightly earlier and turns into a **gametocyte.** These are of two forms, generally easily distinguishable by the distribution of the melanin within them. The male form, or **microgametocyte,** has a large nucleus, lightly staining protoplasm, and small pigment granules more or less evenly distributed, while the female form, or **macrogametocyte,** has a smaller nucleus, more deeply staining cytoplasm, and coarser granules aggregated around the nucleus. In *P. immaculatum* we find the same differences in nucleus cytoplasm and melanin, but the animals take on a characteristic bent sausage-shape within the corpuscle, being then termed the " crescents," and so are clearly distinguished from trophozoites and schizonts in all stages of growth. No further changes are undergone and no development is possible on the part of the gametocytes until they are transferred to the next host, a mosquito.

The next thing, then, is to see how the mosquito becomes infected. The female mosquito lives by sucking the warm blood of mammals, including man, and in order to do this is furnished with a very complex instrument, the proboscis. This is composed of seven distinct parts, all modified from the structures which in other insects constitute the jaws and accessory organs, and together they form a most efficient piercing stylet, as we soon learn to our discomfiture when we go into a mosquito-infected district. Such an apparatus is absent in the male, which cannot, therefore, suck blood. Not only does it form a piercing organ, but it is so constructed that when it reaches a small blood-vessel the parts can be closed together and form a tube leading to the mouth. Behind the mouth is a suctorial pharynx, by means of which a quantity of blood is drawn up into the stomach of the mosquito. Should the female stab a person infected with malaria it automatically sucks up with the blood, corpuscles containing the parasites in different phases of development. In the stomach all stages of the parasite are digested with the blood save only the gametocytes, and these are not merely left undigested, but actually stimulated to activity and assume a motile amœboid form. In this country we have a species closely related to the mosquito *Anopheles*, namely, the gnat *Culex pipiens*, also capable of stinging human beings. *C. pipiens* is the intermediary in a malaria fever, avian malaria, confined entirely to birds. So marvellously exact is the inter-relationship between the parasite and its hosts that on the one hand the gnat cannot be infected with human malaria or ague, nor on the other hand can the mosquito carry avian malaria, although the parasites in the two cases are practically identical in appearance and life history. Each species is capable of spreading only the particular disease that affects either the man or the bird.

Still within the stomach of the mosquito the nucleus of the macrogametocyte undergoes an unequal division, and the smaller daughter nucleus surrounded by a minute quantity of protoplasm is extruded from the cell as the so-called "**polar body.**" After this process of **maturation**, or ripening, the cell is ready for fertilisation, and so is now a **macrogamete.** Microga tocy

The changes in the microgamete are more complex. Its nucleus enlarges, and after the cell has passed through a short phase of activity, putting forth and withdrawing pseudopodia, it breaks up by a kind of multiple fission into six or eight masses. Each of these consists of a karyosome surrounded by chromatin granules. They take up a position near the periphery of the protoplasm, which gives rise to usually six long actively moving filiform processes. Into each of these a karyosome migrates, occupying a central position, while its attendant chromatin grains are scattered along its length.

The remaining protoplasm with the pigment and odd karyosomes

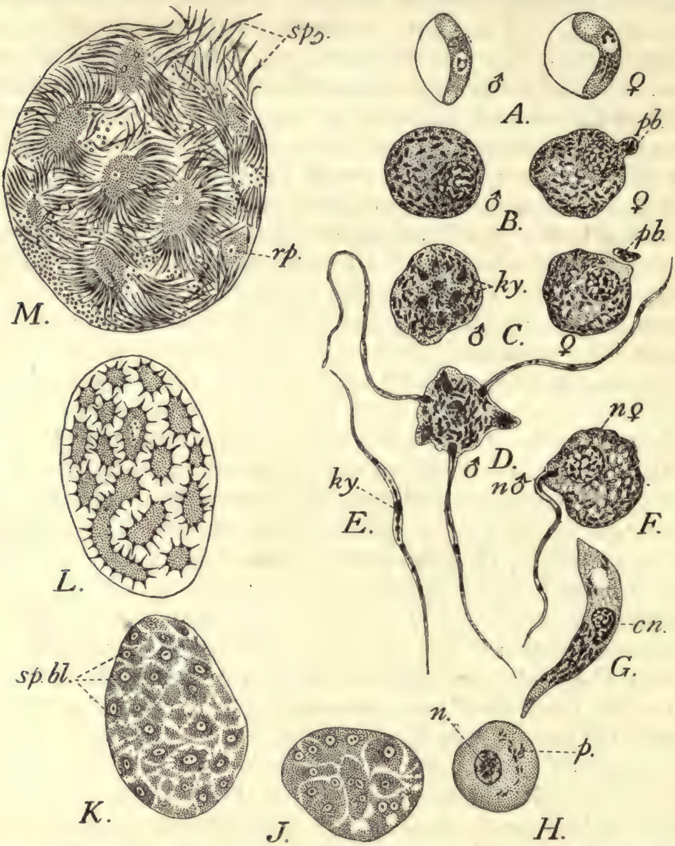


FIG. 46.—Figures illustrating the stages of the life cycle of the malarial parasite found in Anopheles.—From Bourne.

A., crescent-shaped gametocytes of *Plasmodium immaculatum* of pernicious tropical malaria; ♂, the microgametocyte; ♀, the macrogametocyte. *B.*, further stages in the development of ♂ the microgametocyte and ♀ the macrogametocyte of *Plasmodium vivax*; the nucleus of the macrogametocyte has divided unequally to form a polar body, *pb*. *C.*, the nucleus of the microgametocyte has broken up into eight karyosomes, *ky.*, each surrounded by a ring of chromatin granules; the polar body has separated from the macrogametocyte. *D.*, formation of microgametes from the microgametocyte. *E.*, a single microgamete; *ky.*, the central karyosome. *F.*, fertilisation of the macrogamete by the microgamete; *n.* ♂, male pronucleus; *n.* ♀, female pronucleus. *G.*, the motile zygote or oökinete; *cn.*, fertilisation nucleus. *H.*, the oökinete (oöcyst) surrounded by a very delicate cyst wall, at rest in the tissues of the wall of the stomach of the mosquito; *n.*, nucleus; *p.*, pigment. *J.*, multiplication of nuclei in the oöcyst. *K.*, the protoplasm of the oöcyst has divided into numerous sporoblasts, *sp. bl.*, each containing a nucleus. *L.*, early formation of sporozoites from the sporoblasts. *M.*, a ripe oöcyst full of minute sporozoites, *spz*, which are escaping by the bursting of the cyst; *rp.*, residual protoplasm containing an abortive nucleus (*B.–G.* after Schaudinn, the remaining figures after Grassi. The figures are not all drawn to the same scale).

constitutes the residual protoplasm, and plays no further part in the life history. The filiform bodies so formed are the **microgametes,**

and they move about actively when they become free. When one approaches a macrogamete this cell puts out a small protuberance, the "cone of reception," generally from that part of the circumference nearest the nucleus, and to this the microgamete adheres. Gradually the microgamete is absorbed, and its male pro-nucleus travels to a position near the female pro-nucleus. Shortly after this fertilisation is completed by the fusion of the two pro-nuclei to form the **synkaryon** or fertilisation nucleus. A single cell thus results, which is the zygote, but, as it enters into a motile stage in *Plasmodium*, it is frequently spoken of as the **oökinete.** This leaves the alimentary canal of the mosquito by boring through the epithelial lining of the wall of the stomach and embedding itself in the submucosa. Here it secretes around itself a fairly soft cyst, the **oöcyst**, and becomes truly parasitic on the mosquito, feeding on its juices and increasing in size until it forms a knob as large as a grain of millet projecting on the outside of the stomach. The formation of the zygote in *Plasmodium* differs considerably from that in *Monocystis*, for it results from the union of two gametes very different in appearance; a male or microgamete, and a female or macrogamete. Thus it constitutes an example of **Anisogamy** or the fusion of dissimilar gametes, **Anisogametes.**

After a growth period the oökinete enters on a phase of asexual reproduction, leading to the formation of sporozoites. Its nucleus and cytoplasm divide up, producing a number of masses known as the **sporoblasts,** not completely isolated from one another, but united by fine protoplasmic strands and leaving a small portion of residual protoplasm. The sporoblast in turn undergoes multiple fission; a very large number of daughter nuclei are formed, which take up a peripheral position, and a corresponding number of delicate processes are given, into each of which a nucleus migrates. The residual protoplasm breaks down in each case, setting free an enormous number of very minute sporozoites. Finally, the oöcysts burst, releasing the sporozoites into the blood stream of the mosquito, where they are carried about until they come to the salivary glands. They leave the blood at this point and accumulate in vast numbers in the gland.

Now when the mosquito bores into a small vessel to suck the blood it injects a drop of saliva through the proboscis into the wound, and this has the effect of preventing the blood from coagulating. It is very obvious that if the *Anopheles* happens to be infected a great many sporozoites get poured into the wound with the saliva, and so the man becomes infected in this manner. Thus the whole cycle is ready to start all over again. An interesting point in this connection is that the asexual production of the sporozoites

in the mosquito takes some days, and so if a person is stabbed inside this time, unless the mosquito was previously infected, no harm follows, and this has been shown experimentally.

Various precautionary measures are adopted to prevent the spread of these diseases. Firstly, the number of mosquitos in an area may be reduced by removing all small puddles and accumulations of water in old cans, barrels, etc., for it is only in still water that the eggs of the mosquito are laid and the larvæ live. Larger areas of stagnant water can often be dealt with by pouring a little petrol upon them ; this spreads out over the surface and forms a thin film that effectively prevents the mosquito larva or pupa from coming to the surface to breathe, and so kills it. Various ointments may be smeared over the exposed parts, which tend to reduce the number of bites, and, most important of all, an infected man must be isolated at once and kept in curtained rooms from which mosquitos are rigidly excluded.

The two parasitic protozoa we have just studied illustrate several of the main characteristics of parasites in general. In the first place, owing to the peculiar conditions under which they live, they are for the most part devoid of all adaptations for a free-living and food-seeking type of life : they are inactive, save for certain limited periods, and consequently lack organs of locomotion ; their food is already in an assimilable form, so they do not possess cytostome, cytopharynx or food vacuoles. The result, therefore, is a greater or less degree of **simplification,** or better, perhaps, **degeneration,** of structure as compared with free-living forms. Lastly, their immobility, although satisfactory in some ways, is a distinct bar to their reinfecting fresh hosts, and so maintaining the species. In *Monocystis* the transference of the spores to another worm is largely a matter of pure chance, and even in *Plasmodium* chance plays a large part, and it is necessary to ensure that any mosquito biting an infected man should itself become infected, and should subsequently reinfect in turn. Thus it is not merely necessary to reproduce, but also desirable that the mode of multiplication should also serve as a **means of dispersal.** The element of chance in both cases is met by a typically parasitic phenomenon, the production of an enormous number of young. In *Monocystis* also, in order to withstand the weather changes, the spores are provided with a tough resistant envelope that can protect the sporozoites and keep them alive. Some such protected stage is often met with in parasites, but not invariably, for in some, as in *Plasmodium,* where the parasite never lives outside the body of its hosts, the second host that has been acquired obviates the necessity of providing against the inclemencies of the weather.

In *Plasmodium,* moreover, two different forms have been evolved, which have been termed the **multiplicative** and the **propagative** forms respectively; the former serves to multiply in the host, and so bring about a thorough and continuous infection, and the latter serves to infect new hosts. The trophozoites in the blood of the vertebrate by multiple fission produce merozoites or **agametes,** serving exclusively for **self-infection.** Such part of the life history is termed schizogony, and the trophozoites known as schizonts. The gametocytes in the stomach of *Anopheles* produce well-differentiated anisogametes, and these by syngamy form zygotes. The multiple fission of the zygotes leads to the formation of sporozoites, and these are utilised for **cross-infection.** We distinguish this part of the life cycle as sporogony, and the gametocytes may be termed sporonts. *Plasmodium* then is also digenetic, exhibiting in a marked form "alternation of generations," one sexual alternating with an indefinite number of asexual generations.

CHAPTER VI

THE CŒLENTERATA

A Simple Cœlenterate, *Hydra*—A Compound Cœlenterate, *Obelia*.

FROM the single-celled Protozoa we now ascend the first step in the scale of animal life and turn to the Metazoa or multicellular forms. These are animals whose many cells are arranged in at least two layers, which are differentiated in structure and function. The first phylum of the Metazoa with which we are now concerned is the **Phylum Cœlenterata** and *Hydra*, a fairly widely spread genus, furnishes a good example of a simple, little specialised type.

A Simple Cœlenterate—*Hydra*.

The various members of the genus *Hydra* are all inhabitants of fresh water, hence their name of "fresh water polyps," and are to be found adhering to aquatic plants and other submerged objects in our ponds, ditches and streams. Three species, not differing in essentials but only in details of structure, are commonly to be met with in this country: *H. viridis* is of a bright green colour; *H. vulgaris* (or *H. grisea*) is of a pale greyish colour; and *H. oligactis* (or *H. fusca*) is dark yellow or brown. An examination with a hand lens is sufficient to show that the colouring matter in the first and last is in the inner parts, and that the outer layer of the body wall is transparent and practically colourless. The animals vary greatly in appearance, according to the extent they are stretched out. In a fully expanded condition they appear as long, slender, cylindrical threads, from 6 to 7 mm. in length, attached by one end and bearing at the other a circlet of much finer long filiform processes, the **tentacles,** varying from six to ten in number, and these may extend as far again beyond the body. The *Hydra* adheres by a flattened plate-shaped foot or **basal disc,** and at its distal end, within the whorl of tentacles, is a low conical projection, the "**oral cone**" or **hypostome,** in whose centre is a circular opening, the mouth. The whole is exceedingly contractile and extensile and very sensitive, the slightest shock causing it to contract both its body and tentacles

until it appears as a small jelly-like blob. If left undisturbed it will gradually expand again, throwing out its tentacles, which wave about in the water in search of prey. These movements are not the only ones exhibited, for although usually fixed it is able to move from place to place. When it does so it lengthens out and bends over to one side, attaching itself to the substratum by means of its tentacles or mouth some way from the foot. The latter is then released and brought up nearer to the tentacles, where it becomes fixed, so that the animal has thus moved a short distance. This may be repeated several times, and so slow progress is possible in a manner recalling that of a looper caterpillar. All sorts of intermediate conditions between the extremes of extension and contraction may be seen, sometimes limited to one or other end of the body, so that the cylinder is not of equal thickness throughout. Individuals may sometimes be seen in the process of budding, with tiny daughter forms growing from them, or several knob-like projections, the reproductive organs, may be present on the top two-thirds of the body.

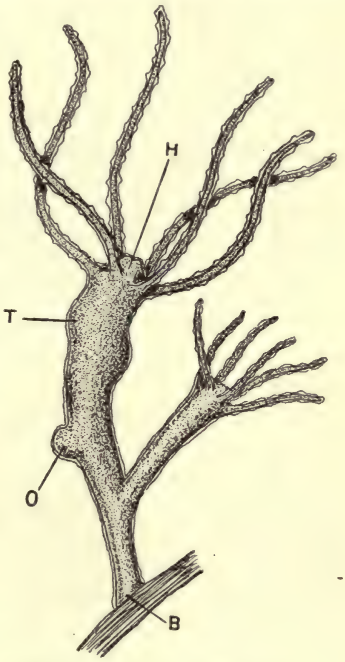


FIG. 47.—*Hydra*, with bud and gonads.

B., basal disc ; H., hypostome ; O., ovary ; T., testis.

A longitudinal section shows that the mouth, the sole external aperture, leads into a hollow cavity coextensive with the body, which is therefore a very minute tube. The tentacles are also hollow, being but long attenuated outgrowths from the body wall. This central hollow is the gut cavity or **enteron,** termed also the **cœlenteron,** to indicate that it corresponds to both the body cavity (cœlom) and gut cavity (enteron) of the higher animals, and this particular type of structure is fundamentally characteristic of the whole phylum, hence its name. Another common feature of the Cœlenterata is exemplified by *Hydra* in the simplicity of its structural plan. If its main axis be marked out by an imaginary line drawn through the mouth and the centre of the basal disc, we find that the tentacles are arranged around it radially, *i.e.* they are related to the axis, as are the radii to the centre of a circle. This is a condition we term

radial symmetry, which is not only general in Cœlenterata, but also tends to be assumed by all animals adopting a fixed mode of life. We cannot speak of anterior and posterior ends or dorsal and ventral sides, but only of **oral** surface, *i.e.* on the side of the mouth, and **aboral,** *i.e.* on the side opposite to the mouth. This type stands strongly contrasted with that in ourselves and the frog, in which the parts are only symmetrically disposed with regard to one plane passing through the long axis, cutting the body into right and left halves, which in consequence we term bilateral symmetry.

Hydra can easily be kept under observation in water in a watch-glass, and if some "water-fleas" (small Crustacea, Daphnids) be added their capture can be watched. The tentacles are widely spread out, forming a primitive kind of net, and sooner or later a water-flea comes into contact with one of them. Immediately it does so it comes to a standstill and all movement ceases, as if it were paralysed, and it remains adhering to the tentacle. This gradually shortens down and bends over so that the animal is brought to the mouth, which enlarges and takes it in, removing it from the tentacle. It is passed inside into the enteron, and for some time causes a distinct swelling in the body of the *Hydra*. Here it is digested, and later the shell and other indigestible residue are ejected through the mouth.

The animal is so small that its structure cannot be made out by dissection, as in the case of the frog, and it has to be studied by means of sections and by isolating the cells. A transverse section of *Hydra* shows that the body wall is composed of two layers of cells. The outer layer, or **ectoderm,** is thinner, and consists of a number of cells tightly packed together, forming a very efficient covering for the animal. These cells, as we shall see later, are more or less cone-shaped, with their bases outwards, and so a series of spaces are left between their inner ends. The interstices are not left empty, however, but are filled with smaller cells. Inside the ectoderm, and so forming the lining of the gastral cavity, is the second layer of cells, the **endoderm,** or better, the **entoderm.** This is composed of much larger, more columnar cells, but, like those of the ectoderm, they are radially arranged. Between the ectoderm and entoderm is a layer of structureless jelly-like substance, the **mesoglea,** forming a sort of strengthening sheath, the **supporting lamella.** Cells may occasionally be found in it, but it should be borne in mind that such cells do not originate in it, they migrate into it from the other layers. It cannot then be regarded as a cell layer, but simply as a sheet of jelly secreted by the ectoderm and entoderm. In *Hydra* it remains quite thin, but in the "jelly-fish" it is enormously thickened, forming the main bulk of the body. This type of body wall, consisting of

only two cellular layers, ectoderm and entoderm, is designated two-layered or **diploblastic,** and is characteristic of cœlenterates. In order to examine the structure of the layers more fully we may either crush an individual under a cover slip by means of a tap with a pencil, or, better still, immerse it for a short while in a macerating fluid.*

We have already seen that the ectoderm is composed of two groups of cells, those forming the main epithelium and those in the interstices, and we can now study them more in detail. The larger

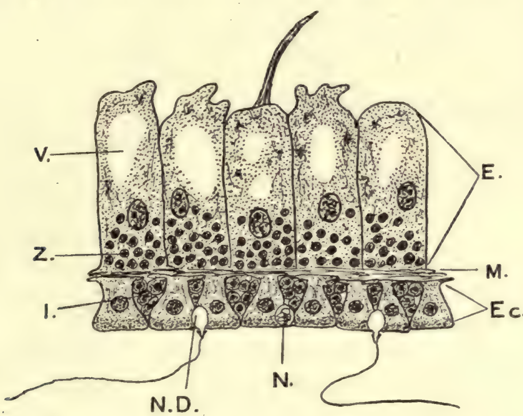


FIG. 48.—Diagram of a transverse section of part of body wall of *Hydra.*

E., entoderm ; Ec., ectoderm ; I., Interstitial cells ; M., mesoglea ; N., nematocyst ; N.D., discharged nematocyst ; V., vacuole ; Z., zoochlorellæ.

cells are known as the **epithelio-muscular cells,** and are roughly cone-shaped. Their outer sides, *i.e.* the bases, are very firmly joined together, so that it is a matter of difficulty to isolate them save in groups, and they are, moreover, covered by a thin homogeneous cuticle. Their inner ends, the apices, are blunt and give off fairly long processes, running transversely to the long axis of the cell. These protoplasmic filaments are the portions of the cell especially set aside for contraction, and hence distinguished as the **muscle processes.** They lie embedded in the mesoglea, and careful examination reveals the presence in them of minute **myofibrillæ,** the specialised contractile elements. Thus the ectoderm furnishes *Hydra* with an external layer of longitudinally running muscles, by the contraction of which the shortening of the body is brought about. The body of

* *E.g.* Schneider's fluid, one part of ·02 % solution of osmic acid and four parts of 5 % solution of acetic acid mixed together. The animal requires to be immersed from three to five minutes and then handled with care, for it disintegrates readily.

the cell is composed of a fairly clear vacuolated cytoplasm, in which are a few coarse granules and a network of delicate fibres, continued through the apex of the cell into the myofibrils of the muscular processes. A large spherical vesicular nucleus with well-marked chromatin threads and one or two distinct nucleoli is situated near the middle of the cell. In the basal disc the ectoderm cells are slightly modified, are columnar in shape, and fitting close together leave no interstices. They are very granular, containing minute droplets of a sticky secretion, which, when passed out, enables the foot to adhere to the substratum. These cells are, therefore, not merely musculo-epithelial, but also glandular in character. The ectodermal cells in the tentacles also are a little flatter than in the body wall, and have very markedly developed muscular processes. They are so closely set together that there are no spaces between their inner ends.

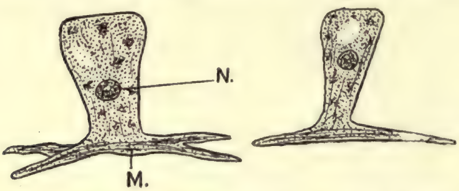


FIG. 49.—Epithelio-muscular cells of *Hydra*.
M., myoneme fibrillæ; N., nucleus.

The remaining cells of the ectoderm, termed from their position the **interstitial cells** or **sub-epithelial cells,** are small and round and tightly packed together. They form as it were a reserve of unspecialised cells, from which other cells of the ectoderm can be replaced, and they give rise to four very distinct types.

1. The most numerous and striking cells arising from the interstitial ones are the wonderful structures known as the "nettle cells," or **cnidoblasts,** in each of which is enclosed a complicated highly-refractive capsule, the "stinging capsule," or the **nematocyst.** These capsules contained in their parent cells are to be found distributed generally in the ectoderm with the exception of the basal disc. In the tentacles they are particularly numerous, being arranged in groups, the so-called nematocyst batteries, which give the tentacles a knobby appearance. The cnidoblast is not found free in the ectoderm, but completely embedded in one of the musculo-epithelial cells—a cell within a cell, recalling in some respects a parasite.

The cnidoblast consists of a thin layer of protoplasm enclosing the capsule, and in it is situated a nucleus. From the outermost part of the cell wall comes off a short slender bristle-like projection, the **cnidocil** or **trigger process.** It pierces the musculo-epithelial cell and cuticle and sticks out beyond the body wall. It recalls the process of a sense cell, and, like it, is receptive and capable of

conveying a message into the cell. The nematocyst is formed within the cnidoblast as a metaplasmic product, and takes the shape of a refringent oval capsule with a tough, probably double wall. At its outermost point the capsular wall is pushed in or introverted to form a narrow tubular ingrowth which extends nearly the length of the nematocyst. It then quickly narrows down and is continued as a very fine thread spirally coiled around the tubular ingrowth. The remainder of the inside of the capsule is filled with a semi-gelatinous fluid which renders the whole tense and turgid. Under suitable conditions of hunger, etc., if a small water animal touches the cnidocil it causes the nematocyst thread to be shot out with explosive violence. The semi-gelatinous fluid is apparently very

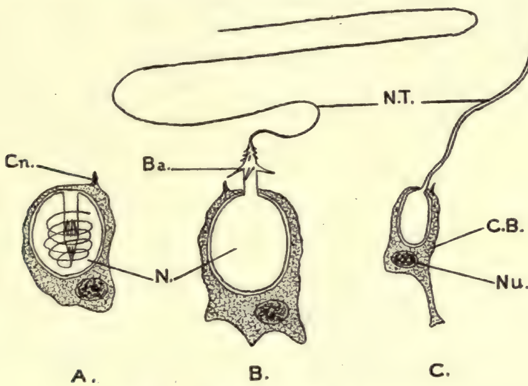


FIG. 50.—Cnidoblasts of *Hydra*.

A., large variety undischarged; B., large variety discharged; C., small variety discharged. Note small size, absence of barbs and thickness of thread.

Ba., barbs; C.B., cnidoblast cell; Cn., cnidocil or trigger process; N., nematocyst; Nu., nucleus of cnidoblast; N.T., nematocyst thread.

hygroscopic, and the slight disturbance of the cnidocil in some way or other allows it to absorb water, with the result that a pressure is produced practically instantaneously and the thread is ejected, being turned inside out in the process. When discharged the nematocyst appears as an empty capsule on one side of which is a projection like the short handle of a whip, often bearing several barbs large and small, continued on as a delicate thread-like lash many times longer than the cell itself. These serve as offensive and defensive weapons, and, as we have seen, there is force enough in the thread when discharged for it to penetrate into the body of the water-flea. The consequent paralysis of the animal is presumably brought about by the thread carrying with it a small quantity of an irritant poison. The presence of this poison has not been shown in *Hydra*, but some of its allies, certain sea-anemones and jelly-fish, when they sting a

human being, produce a result similar to the sting of a nettle, only it may be a great deal more severe.

When once discharged the nematocyst thread cannot be introverted again, and so is useless and shed. They must, therefore, be replaced constantly, and so we can find in the interstitial cells, especially in the distal parts of the body, many that have capsules in different stages of formation within them. They are used up most rapidly on the tentacles where, however, there are no interstitial cells, and it is not quite clear how the replacement is effected. It is almost certainly brought about by the migration of the fairly young cnidoblasts, although this has not been demonstrated. Two varieties of nematocyst are met with in *Hydra ;* one, the larger, is of an oval form similar to that described above, and the other is smaller, a longer oval, and the thread, when it is discharged, is thicker, shorter and without barbs at the base.

The nematocyst is a structure confined to the Cœlenterata, but widely, if not universally, distributed in that phylum, and retaining throughout the same fundamental structure, although the size, proportion of its parts, and the presence or absence of barbs varies from species to species. It forms, as can readily be seen, a very efficient weapon.

FIG. 51.—Primitive nerve cells of *Hydra*, adapted from Schneider.

2. The second type of cell produced by the interstitial cells is the nerve element. All the cells of *Hydra* appear to be very sensitive, but the nerve cells are those in which this property is most highly developed. They are small, bipolar or multipolar primitive ganglion cells, and all their processes may branch freely, but do not appear to be structurally differentiated into axons and dendrons. Around the mouth they are rather more numerous than elsewhere, but even here they do not form ganglia or aggregations, being merely scattered about in the mesoglea. In this way they form a loose network of a nervous nature, serving to keep all parts of the animal in communication with one another, and so co-ordinating the activities of the animal as a whole.

3. A few cells on the hypostome and the basal disc appear to b

of a sensory nature. They are long thread-like cells situated between the epithelio-muscular cells and branching out at their inner ends like the nerve cells, to which no doubt they are closely related.

4. Lastly, it is to the interstitial cells that we have to look for the primitive germ cells. *Hydra* is **hermaphrodite,** that is to say, the one individual produces both spermatozoa, the male cells, and ova, the female cells. We express the same idea when we term it **monœcious,** *i.e.* of one sexual form as opposed to most of the higher animals, which are **diœcious,** *i.e.* of two forms, male and female. The spermatozoa are aggregated in large numbers, producing one or more enlargements, the testes, lying in the oral third of the body beneath the ring of tentacles. The ova when fully ripe are very large single isolated cells, which also produce swellings, the ovaries, situated about the middle of the body below the testes.

The entoderm of *Hydra* is composed in the main of three types of cells :—

1. Again, the main part is composed of musculo-epithelial cells which are, however, much larger and more columnar than those of the ectoderm. Their muscular processes are also embedded in the mesoglea, but are arranged transversely to the long axis of the body, *i.e.* circularly, and are not so strongly developed. The edge of the cell towards the gastral cavity is of indefinite shape and capable of putting forth amœboid processes which can seize small pieces of the food. The cytoplasm is very vacuolated, sometimes containing one large vacuole, and also granular with tiny particles of food in it. In *H. viridis* and *H. oligactis* there are also present in the cell numerous minute ovoidal capsules of a bright green or yellow colour, according to the species, lying towards the basal part of the cell. They are really minute plants, Algæ, that have made these cells their dwelling-place. A noticeable vesicular nucleus with a distinct nucleolus is also present, and usually more or less basally situated.

2. The second type of cell is secretory, and such glandular cells are to be found fairly generally scattered, but most commonly in the neighbourhood of the hypostome. They are much like the other cells, but contain large droplets of a slimy or albuminous nature.

3. Lastly, we find in the entoderm a certain number of interstitial cells wedged in between the bases of the epithelio-muscular cells, but they are not nearly so plentiful as in the ectoderm, and only occur here and there.

The limited movement of *Hydra* as a whole, and that of the tentacles, has already been mentioned. Its feeding is of an interesting type. When the prey reaches the gastral cavity it comes under the action of the secretion of the gland cells which contain

enzymes allied to trypsin. As a result of this activity the prey disintegrates, and as the small pieces of it float about in the cavity they are seized by the epithelio-muscular cells and engulfed in the same manner as *Amœba* ingests its food. They are then digested in the cell. Thus we find two distinct types of digestion within the body of *Hydra ;* firstly, **intercellular digestion** in a cell-lined gastral cavity, the only kind met with in the higher metazoa ; and secondly, the **intracellular digestion,** in which the food is broken up within the cell itself as in the Protozoa. The only phenomenon allied to this latter type in the higher animals is that we have already dealt with in the case of the white blood corpuscles of *Rana*, termed phagocytes, for in this case the bacteria are swallowed and eaten by the cells. Any insoluble residue, including starch, for apparently *Hydra* does not secrete a starch-splitting enzyme, is voided through the mouth, which therefore functions also as an anus.

Another phenomenon calls for notice here, and that is the relation between the tiny green plants and the entoderm cells. These green algæ, when they are included in an animal cell, as they are in certain protozoa and worms, are termed in general **Zoochlorellæ,** and the particular species particularly associated with *H. viridis* is *Chlorella vulgaris*. They are in no sense parasites, for they are not detrimental either to the structure or function of *Hydra ;* in fact they are quite the reverse. The animal not only lodges and protects the algæ, but produces as waste products carbonic acid gas and various nitrogenous matters which serve the plant as food. On the other hand, the plant removes these waste materials for the animal, and in its turn makes Oxygen, which is of use to *Hydra*, and perhaps also certain carbohydrates. Certain it is that a *H. viridis* freed of its *Chlorellæ* does not live so vigorously as with them. Thus we have a living together which results in a mutual benefit to both parties concerned, and this, which we term **Symbiosis,** is to be sharply distinguished from parasitism.

Respiration and excretion in *Hydra* other than that just dealt with appear to be carried out as in *Amœba*, by diffusion over the general surface of the body, and there is no special organ for the performance of either function.

Reproduction in *Hydra* takes place, as we have seen, by two methods, by budding and by the production of gametes. In asexual multiplication there is first of all an increase in the interstitial cells, and then the two layers of the body wall grow out into a tiny knob-like projection whose internal cavity is continuous with that of the parent. At first it is rounded, but a series of tiny sprouts at the distal extremity mark the beginning of the tentacles, which soon grow. In the middle of these appears an opening, the mouth,

and so we have produced a tiny *Hydra* growing out from the body of the parent with which its layers and cavity are directly continuous. When conditions are favourable, more than one bud may be formed; indeed, specimens are sometimes met with in which the buds themselves have budded, so that temporary associations are formed. Sooner or later, however, the daughter individuals drop off and lead an independent life. *Hydra* exhibits another phenomenon somewhat allied to this production of buds, and although it can hardly be considered as an ordinary means of reproduction, doubtless plays its part in cases of injury. If an individual be cut into a number of pieces, provided they are not too small, and contain fairly representative parts of both ectoderm and entoderm, each piece is capable of regrowing into a complete animal. This is a power we term Regeneration, which is fairly common among lowly organised beings, but becomes more and more limited as we ascend the animal scale.

Sexual reproduction also occurs as a normal method in *Hydra*, but no alternation or definite relation between it and the asexual has been shown to exist, and it is the more uncommon of the two. The testes at first consist of a mass of interstitial cells which at a certain stage are termed the **spermatogonia.** These divide, producing two **spermatocytes,** and each of these in turn gives rise to four sperms. The adult spermatozoa are composed of a small oval head to which is attached a fairly long vibratile tail. They are aggregated in large numbers between the epithelio-muscular cells of the ectoderm, and so form noticeable colourless swellings, the testes. When quite ripe the ectoderm cells split, releasing the free-swimming sperms into the water. Like the testes, the ovaries also commence as a collection of intestitial cells which form the **oögonia**, but only one of these is destined to become the sex cell. This divides up, and one of the daughter cells, *i.e.* the **oöcytes,** so produced assumes a central position in the mass. It sends out pseudopodia and feeds upon its sister cells much in the same way as an *Amœba* ingests its food. The result of this feeding is that the cell grows to a relatively enormous size, and the products of digestion are stored up within it in the form of numerous tiny spherical masses, the **yolk spheres** or **deutoplasts.** This amœboid stage is not at all common in developing ova among animals, and when it is ended the oöcyte withdraws its pseudopodia and rounds off. It then undergoes two successive unequal divisions, giving off two tiny masses of protoplasm, each with a certain amount of nuclear material, the **first** and **second polar bodies,** and so becomes a ripe ovum ready for fertilisation. By this time it has been surrounded by a thin gelatinous layer, and increased so much in size that it has caused the ectoderm cells to split, exposing part of its surface to the water ready for the sperm. Fertilisation

is effected in the normal manner by the penetration of a single spermatozoon, and the fusion of the two pronuclei to form a zygote with its segmentation nucleus.

The process of cleavage or segmentation now sets in, and

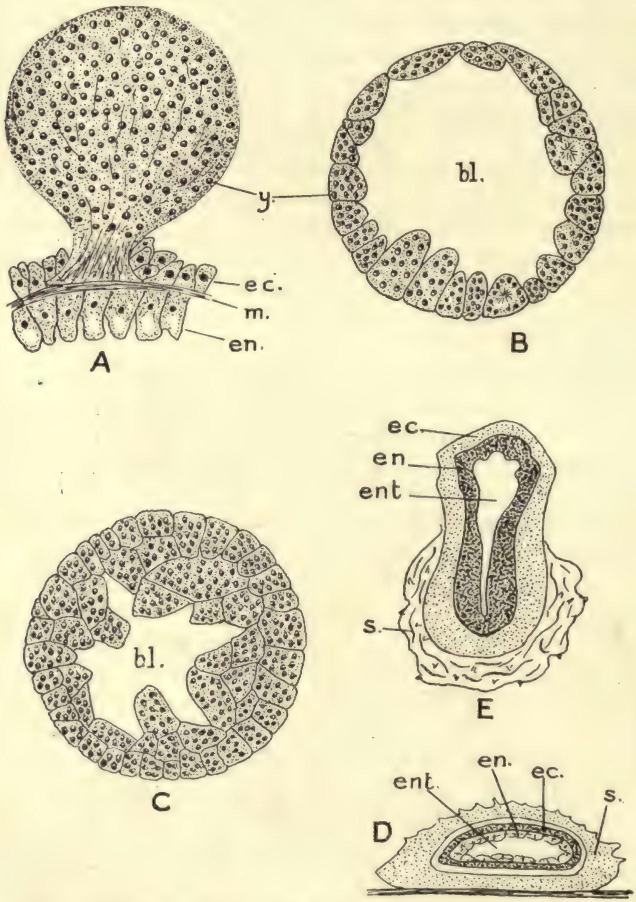


FIG. 52.—Development of *Hydra*, adapted from Brauer.

A., the mature ovum full of yolk granules and attached to the parent ; B., section through the blastula, some of whose cells are already beginning to pass inwards ; C., section through gastrula showing the irregular entoderm cells commencing to fill the blastocœl ; D., the embryo within protective sheath flattening out and the entoderm cells arranged to form a layer around the enteron; E., embryo escaping from sheath ; D. and E., less highly magnified than remainder.
bl., blastocœl ; ec., ectoderm ; en., entoderm.

it is during this period in *H. viridis* that the ovum becomes infected with the green algal cells. Two meridional divisions cut the original cell into four, and a subsequent equatorial split into eight, cells

surrounding a central cavity. Ultimately a hollow sphere of cells is produced, the **blastula,** in which is a large central space, the **blastocœl** or **segmentation cavity.** The blastocœl is next filled by cells derived from the periphery in two ways. Some of the outside cells divide tangentially, and the more centrally situated of the two daughter cells pass inwards, a process called **multipolar delamination,** because it occurs at many points ; others of the cells from different parts migrate into the centre, and this is termed **multipolar immigration.** Finally, as a result of these two processes, the sphere becomes solid. The ingoing cells carry with them practically all the yolk spheres, with the result that the embryo comes to consist of an outer layer of more clear cells, the ectoderm, surrounding an inner solid mass of granular cells, the entoderm, and in this way the diploblastic condition is attained. This secretes around itself a double-walled sheath, the outer layer being horny and covered with spinous projections, and the inner, membranous. All these changes take place while the egg is still attached to the parent, but now it drops off and falls to the bottom of the pond. After a period of rest the entoderm cells become arranged to form a layer around a central cavity, the enteron or gastral cavity, and then the capsule breaks, allowing the animal to creep out. At first it has no tentacles nor mouth, but these soon appear much in the same way as they do in a bud, and so we have produced a new *Hydra*.

This, then, completes the life history of a very simple Metazoon, and although a primitive and, perhaps, even a degenerate form, it serves as a type of the Phylum Cœlenterata, the majority of whose members are, however, more complex. In some ways it marks a very important step in advance of the Protozoa, the first stage in the direction of that enormous complexity of cellular structure that marks the higher animal.

A Compound Cœlenterate—*Obelia.*

We now pass on to consider a more highly-organised member of the same Phylum, namely, *Obelia*. The genus *Obelia* is a very common one around our shores, and, confined to the sea, it is to be found just below low-water mark, sometimes, indeed, exposed at spring tides, growing on stones, wooden piles and other submerged objects. *O. geniculata,* perhaps its most common species, is frequently encountered as a pale greyish-brown moss-like growth forming large conspicuous patches on the long fronds of the oar weed (*Laminaria*). Its plant-like appearance is common among the Hydrozoa, the class of the Cœlenterata to which it belongs, and, in consequence, these animals have long been known to naturalists

as plant-animals, Zoophytes. Quite small, as a general rule, these organisms nevertheless when viewed alive under even a low magnification form some of the most beautiful objects to be met with in the animal kingdom. Closely adherent to the seaweed frond will be found a network of fine threads which constitute a kind of root, the **hydrorhiza,** serving for attachment. From this arise a number of thread-like stems, the **hydrocauli,** which on closer examination are seen to give off a number of small lateral branches, each one terminating in a tiny knob. Even a low magnification will reveal the fact that each of the small lumps is in reality a tiny flower-like hydriform being, closing in response to the slightest touch when living, and variously termed a **hydranth,** a **polyp** or a **zooid.** Thus we have a compound organism composed of a large number of hydroid individuals united together by common stems and roots, and such an assemblage we call a **colony** or **stock.** We saw that in *Hydra* sometimes the individual could bud off daughters, and that before these were shed they could in themselves give rise to buds producing a sort of temporary colony, and the stock in *Obelia* is formed much in the same way. A single hydriform being gives rise to a bud which grows upwards, turning the head of the parent to one side and also produces a bud, and this in its turn another bud, and so on. In this way we have produced a long stem, the end of which is always growing, and in *Obelia,* as the buds are produced on alternate sides, we have formed a characteristic zigzag stem with zooids borne on short stalks at its angles. From their mode of origin, too, it will be seen that the gastral cavities of all the hydroids will remain in continuity with one another by means of the hollow stem. The hydrorhiza is also a series of tubes, so that the whole colony, sometimes consisting of an enormous number of individuals, has a series of gastral cavities intercommunicating by means of **gastro-vascular canals.**

In order to keep the stem erect we find that the colony secretes around itself a supporting and protective exoskeleton composed of a horn-like substance, chitin. We distinguish the skeletal substance as the **perisarc** as opposed to the **cœnosarc,** *i.e.* the living parts which it surrounds. In the regions of the hydroids the perisarc expands into cup-shaped receptacles, the **hydrothecæ,** into which the polyps can, and do, completely withdraw when disturbed. Then, too, the perisarc of the stalk joining the hydranth to the main axis exhibits a series of ringlike constrictions or annulations, as may also the main stem itself at these points. The number and arrangement of these differs in various species.

The particular type of individual noticed above is almost exclusively concerned with the procuring, digestion and distribution

of food, and so is spoken of as the **nutritive zooid,** but two other kinds of person are to be found. In the first place sexual reproduction is brought about by a special set of individuals in the form of small saucer-shaped zooids produced as buds by the colony, but afterwards cut off as minute free-swimming jelly-fish or **medusæ,** and these are the reproductive individuals. Secondly, these reproductive forms are not budded from any part of the colony indiscriminately, but only from specially modified hydroids, the **blastostyles,** which have no mouth or tentacles, and consist of a long slender body. Here, then, as a result of the division of labour among its constituent persons, we encounter the phenomenon of **polymorphism,** or the production of different forms of individual in one and the same species. It is even more marked in the case of some of the allies of *Obelia,* and is met with in various groups of the animal kingdom, as, for example, in the social insects, ants and bees. The particular type of polymorphism in the present case, since it involves three varieties of individual, the hydranth, the blastostyle and the medusa, may be called **trimorphism.**

The blastostyles are always to be found in a constant position. Usually they are absent from the upper or younger end of the hydrocaulus, but almost always present lower down. They occur in the angle between the polyp stalk and the main stem (in the axil, as we should say, of leaves) toward the upper side. Each is enclosed in a special urn-shaped investment of the perisarc, the **gonotheca,** which is almost sessile and has not a distinct stalk like that of the hydrotheca.

The structural plan and histology of the whole colony is very similar to that of *Hydra,* but perhaps, on the whole, more simple. The cœnosarc of the hydrocaulus and hydrorhiza consists of a series of tubes which are only loosely connected with the perisarc save at the growing ends of the branches. It is composed of an outer clear layer of ectoderm which lacks cnidoblasts, and an inner more granular layer of entoderm whose cells are sometimes ciliated, and bear flagella in order to assist in the circulation of the nutritive fluid. The two layers are separated by the mesoglea, and in neither are the muscular processes at all well developed.

The nutritive zooid somewhat resembles *Hydra,* but has a circlet of about thirty well-marked filiform tentacles. They are fairly contractile and plentifully supplied with cnidoblasts. Their ectoderm is on the whole similar to that in *Hydra,* but the entoderm, which completely fills them, is composed of a single axial line of peculiar cells. These cells are large and very vacuolated with a nucleus near their centre, and are tough and elastic. The hypostome is enormously developed, forming a dome-like enlargement between the bases of the tentacles. Within, it forms a sort of initial gastral

cavity, almost as large as the proper one whose walls are lined with an entoderm containing a large number of glandular cells. The body of the hydranth calls for no special notice, but it is suddenly constricted at its base, which sits on a kind of perforated shelf at the bottom of the hydrotheca. It is continued through this central hole as a very narrow tubular neck-like portion, the **hydrocope,**

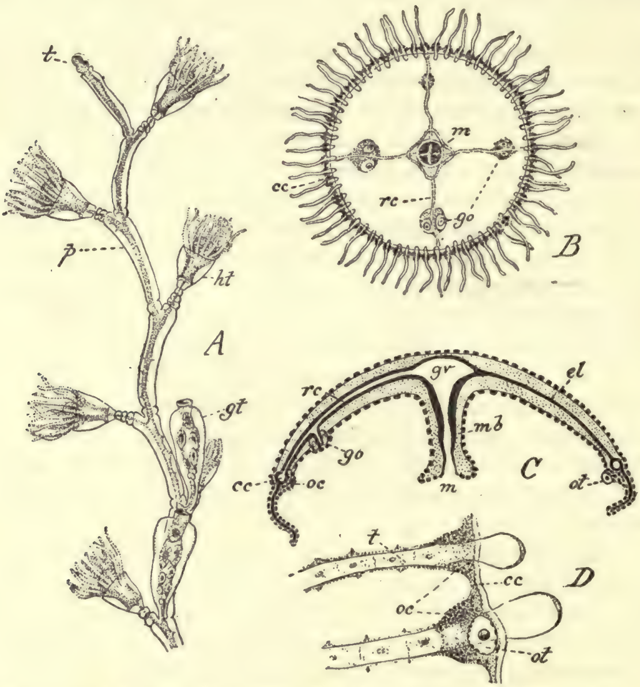


FIG. 53.—*A.*, part of a colony of *Obelia geniculata* magnified.—From Bourne.

ht., hydrotheca containing a hydranth ; *gt.*, a gonotheca enclosing a blastostyle with medusa buds ; *p.*, perisarc ; *t.*, terminal growing point. *B.*, a sexually mature female medusa, seen from below ; *m.*, mouth ; *r.c.*, radial canal ; *cc.*, circular or ring canal ; *go.*, gonads. *C.*, diagrammatic longitudinal section through a medusa ; *m.*, mouth ; *mb.*, manubrium ; *g.v.*, gastro-vascular cavity ; *r.c.*, radial canal ; *cc.*, ring canal ; *e.l.*, endoderm lamella ; *oc.*, ocellus ; *ot.*, otocyst. The section is supposed to pass through a radial canal on the left side and an adradial tentacle on the right. Endoderm black ; mesoglœa shaded ; ectoderm represented by a broken line. *D.*, the bases of two tentacles magnified, showing *oc.*, ocelli ; *ot.*, an otocyst on an adradial tentacle ; *cc.*, ring canal.

which, however, soon swells out and becomes continuous with the cœnosarc. Thus the gastral cavity of each polyp is continuous with the cœnosarcal canal, and so food eaten by any one individual can be utilised for the benefit of the whole. The function of this zooid is purely nutritive, except in so far as its budding to form another hydranth can be looked upon as a kind of reproduction, which in

some senses it is. By this means, of course, more individuals are added to the colony, but new colonies are apparently only formed by the process of sexual reproduction. When living, the hydranths are in a constant state of motion, waving their tentacles about in search of prey, expanding and contracting, so that some of the more brightly-coloured allies of *Obelia* are most beautiful objects and, looking as they do like hundreds of animated flowers, well deserve their name of zoophytes, plant animals.

The blastostyle is a hollow outgrowth of the cœnosarc with an internal cavity continuous with the gastro-vascular canal. It corresponds with a drawn-out body of a hydranth, and has a knob-like enlargement at its distal extremity in place of the hypostome. No indication of mouth or tentacles is to be found, and it is quite incapable of catching prey, so that it is dependent for its food on the nutritive polyps. The relation between it and an ordinary zooid is not so obvious in *Obelia* as it is in certain other members of the same class, in which the medusoid person is actually budded off from an ordinary hydranth. We therefore regard the blastostyle as a highly modified and degenerate polyp, specialised for the production of medusoids. As has been noted, the blastostyle is contained in an urn-shaped expansion of perisarc, the gonotheca, and the two together are sometimes termed a **gonangium.** A succession of hollow buds are produced by the blasostyle, and these gradually grow into rudimentary medusoid persons which after a while become separated off. They undergo a little further development in the gonotheca, but ultimately the top of this ruptures and allows them to escape.

The free-swimming reproductive individual of *Obelia*, the **medusa,** differs very considerably in appearance from either the other zooids or from *Hydra*. It is a small transparent organism about 2 or 3 mm. in diameter, and shaped like a saucer, with a short stout handle in the middle. From its likeness to an open umbrella the outer, convex, or aboral surface is termed the **exumbrella,** and it was by the centre of this that it was attached to the blastostyle. The under, concave, or oral surface is spoken of as the **sub-umbrella,** and bears in the middle the short more or less rectangular handle, the **manubrium,** on the distal extremity of which opens a cross-shaped mouth. The rim of the umbrella is fringed with a row of delicate tentacles, which may be as few as sixteen when the animal is first liberated, but increase to more than a hundred with age. The tentacles are well provided with batteries of nematocysts, which, in the case of some of the larger allies of *Obelia*, are capable of stinging human beings so as to cause considerable pain. At the base of each tentacle, where it is fixed into the umbrella, it enlarges slightly, and is covered by a

patch of pigmented epithelium, in which are a number of sense cells. This area is sensitive to light, and so forms a very rudimentary sort of eye, the **ocellus**.

The mouth leads straight into the enteron, which continues up the manubrium, and at its base, within the thickness of the umbrella, enlarges to form a rounded rectangular cavity, the stomach. From the corners of the stomach four delicate tubes, the **radial canals,** pass out to the periphery, there to open into another tube, the **circular canal,** which runs round the edge of the umbrella. About half-way to the circumference each radial canal has a small downwardly directed sac, around which the germ cells are congregated, forming an outbulging in the sub-umbrella surface, the gonad. In this way we have what is, compared with a polyp, a complex gastro-vascular system, which is throughout lined by entoderm. The radial canals are not isolated, but connected together and with the circular canal by a very delicate double layer of cells, forming a thin sheet known as the **entodermal lamella.** All the remaining part of the thickness of the umbrella is made up by the jelly-like mesoglea, which fills up all the spaces between the external covering ectoderm and the internal entoderm. It corresponds with the mesoglea of the polyp or *Hydra*, and is secreted by the other layers, but is very much thicker.

Like the polyp, the medusa is radially symmetrical about a main axis, constituted by a line passing through the centre of the exumbrella and the mouth. Four secondary axes are marked out by lines drawn through the radial canals, which also pass through the arms of the cruciform mouth. These are distinguished as the **perradii**, and the canals in consequence are sometimes termed the **perradial canals.** The axes formed by bisecting the angles between these perradii are termed the **interradii,** and the eight axes half-way between these and the perradii are the **adradii.** The tentacles at the end of all these different radii, sixteen in number, are the first to be formed, and the medusa may be set free at this stage, but not before and often not until other tentacles have appeared. Each adradial tentacle has not only an ocellus, but in addition another sense organ in the form of a minute spherical sac. This is lined with ectoderm, and the cells at its lowest part possess sensory hairs, while small calcareous particles are present inside. These bodies are the **lithocysts** or **statocysts.** From a somewhat superficial resemblance to the sensory parts of the membranous labyrinth in the ear of higher animals they were formerly termed otocysts, but this is not a good term. There is little doubt that their function is the perception of the position of the animal in space, particularly its orientation with regard to the action of gravity, and hence they are

organs of balance or equilibration. In these structures and in the ocelli we have a decided advance upon the conditions obtaining in *Hydra* or even the polyps of *Obelia,* for here we have definite parts specialised for a particular function, in other words sense organs. In correlation with this sensory system we find that the nervous system also is more highly organised, for in addition to the ordinary scattered nerve cells in the mesoglea there are also developed two much denser rings of these cells around the margin of the umbrella, although even yet we have no definite aggregations to form ganglia. By means of the marginal nerve rings the animal is able to co-ordinate the action of all the umbrella muscles and perform definite swimming movements. If they are cut away the umbrella seems incapable of co-ordinate movement. Even more than this, it has lost all its **automatism,** that is to say, the power of originating the stimuli that bring about muscular contraction, so that it cannot move of its own accord. Thus, although we have an increased development of the nervous system, it is accompanied by the circumscription of the power, for if *Hydra* be cut into pieces each is capable of separate contraction and expansion. In other words, the automatism is diffuse in *Hydra*. Throughout the animal kingdom in general we find that differentiation of structure is accompanied by localisation of function.

Hydranth and Polyp.

Superficially there is little resemblance between the hydroid and medusoid type of person, and yet a closer examination shows that the fundamental structure is the same in both cases. They are constructed upon the same plan, and are to be regarded as homologous. Suppose we imagine a polyp much shortened in its main axis, and at the same time the transverse diameter much increased by the expansion of the narrow rim between the hypostome and the bases of the tentacles, then a slight curvature will produce a medusa-like form. The resemblance is not complete, for, although we should have comparable oral and aboral sides, tentacles, and manubrium, and the same main axis of symmetry passing through mouth and aboral pole, the enteron and mesoglea would differ markedly. The next stage necessary would be the thickening of the mesoglea, which would bring about a reduction in the large gastral cavity, otherwise occupying the whole of the space between oral and aboral surfaces right out to the periphery. If the mesoglea thickened much more over certain areas than others it could lead to the obliteration of the enteron, save in the positions occupied by the stomach and canals and the formation of the entoderm lamellæ, and so we should have the condition of the adult medusa. Needless to say, the medusa

does not arise in this way, for it is formed directly by the modification of a hollow bud from the blastostyle, and is never at any time a polyp. The above stages, however, are not purely imaginary, for we have indications that the gastral cavity is at first extensive, and

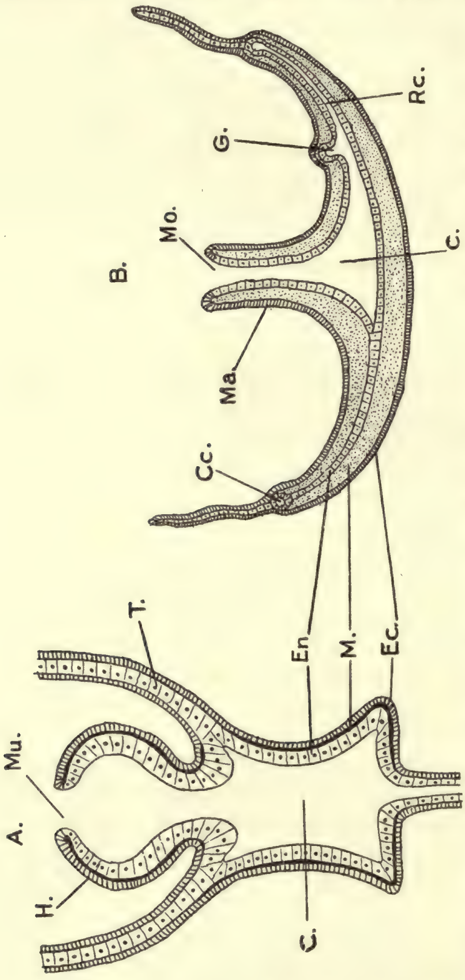


FIG. 54.—Diagram of sections through the hydroid and medusoid individuals of *Obelia* for comparison.

A, hydroid; B, medusoid, the plane of section passing along a radial canal on one side but not on the other. C., cœlenteron; Cc., circular canal; Ec., ectoderm; En., entoderm; G., gonadial outgrowth; H., hypostome; M., mesoglea; Ma., manubrium; Mo., mouth; R.C., radial canal; T., tentacle.

that the entoderm lamella is formed in the way suggested. It serves to show how nearly alike the two forms are, and perhaps we are justified in regarding them as modifications of the one type each adapted for its own particular mode of life. The medusa is a free-swimming wanderer, and needs therefore to have specially developed muscular and sensory systems, which in turn necessitate an increase

of nervous control. Mesoglea is excessively developed, not so much for protection as to lower the specific gravity of the animal to allow of floating. The hydranth, on the other hand, is a fixed form not needing locomotor, sensory and nervous specialisation, but requiring a longer, stalk-like body to hold it up from the ground and a thinner tougher mesoglea for support. The exumbrella of the medusa, which is the part attached to the blastostyle, corresponds to the foot of the hydranth, while tentacles, mouth and manubrium are similar structures in both forms.

When living the medusa swims slowly by a series of sudden contractions of the umbrella, that propel it through the water aboral side foremost, by forcing out the water contained in the sub-umbrella space. It is not capable of active locomotion, being in the main a floating form. The power of contraction lies partly in the epithelio-muscular cells of the sub-umbrella ectoderm, but their efficiency is greatly augmented by a definite ring of **muscle fibre cells** around the margin of the umbrella. These cells are ectoderm cells that have become much modified and their muscle processes greatly enlarged, until ultimately they form almost pure muscle fibres, which sink down into the mesoglea, and so come to take up a sub-epidermal position. Here then we have another advance on *Hydra*, the production of a specially developed ring of muscle elements. The food is caught by the tentacles and conveyed to the mouth as in the polyp, thence it is passed to the stomach and digested. The substances in solution are circulated to all parts by the gastro-vascular canals, and the undigested residue is expelled through the mouth, no anus being developed.

The sexual reproduction in *Obelia* is brought about by these medusoid persons, which are the bearers of the germ cells. They are diœcious, that is to say, the sexes are separate, and any individual medusa is either male or female, but not both, the four gonads in the one case being testes, and in the other ovaries. When first liberated the medusæ show no signs of the sexual cells, and even when the downgrowths of the radial canals, the future gonads, have been formed there is still no sign of the germ cells. It is interesting to note that the oögonia and spermatogonia do not make their first appearance in these gonadial rudiments, but on the other hand they are first discernible in the walls of the manubrium. Thence they migrate along the entoderm of the gastral cavity and radial canals to their definitive position between the ectoderm and mesoglea, where they undergo maturation. It is not until this migration has taken place that we can strictly term the down-growths gonads. In other allied forms the **primordial germ cells** first appear in the hydrocaulus, and then wander to the place where

a medusa is being formed, and then on into the medusa. Such a migration of the germ cells has been observed in a number of other invertebrates, and also in certain vertebrates, in all of which cases the primordial germ cells are first recognisable at some distance from the points at which the gonads will later be formed. Furthermore, in some cases a mother sexual cell is to be distinguished at a very early stage in the cleavage when only a few cells are present. From these facts we may draw a line of demarcation between the ordinary cells that go to form the body, the **somatic cells,** and the cells destined to give rise to all the germ cells, and we also see that the latter are to a certain degree independent of the former, a consideration that is often referred to in discussing theories of heredity.

The medusæ float about in shoals of enormous numbers, and when the germ cells are ripe the gonads rupture, setting the ova and spermatozoa free in the sea where fertilisation occurs. Thus the medusa serves not only for multiplication but also for the dissemination of the species. The zygote undergoes complete and regular segmentation, leading, as in *Hydra,* to the formation of a hollow sphere of cells, the blastula. The cavity within it, the blastocœl, is later filled in a similar way by cells derived from the periphery, but these cells are only produced at one part of the circumference, and consequently the process is described as **unipolar delamination** and **immigration.** Thus arises a solid embryo with an outer layer of columnar cells, the ectoderm, enclosing a solid mass of entoderm cells. This elongates, develops a coating of cilia, and leads an independent life, floating near the surface of the sea. When, in an early stage of its development, before it resembles the adult, an animal lives freely and independently we term it a **larva,** and in the particular case of *Obelia* the larval form is known as a **Planula.** It is quite a common stage in the class Hydrozoa, although missing in *Hydra* itself. Sooner or later the entoderm cells become arranged around an internal cavity, the enteron, which makes its appearance as a slit. The larva then settles down and attaches itself by an expanded **basal disc** to some object in the sea, often, in the case of *O. geniculata,* a frond of *Laminaria.* It sheds its coat of cilia and becomes transformed into a hydroid individual by the enlargement of the distal extremity and the appearance of tentacles, hypostome and mouth. The ectoderm now secretes a tubular investment of perisarc, and in this condition, when it is a simple hydra-like animal with a marked basal or attachment disc, it is termed a **hydrula.** It starts now to grow into a colony : a bud appears some way up the stalk, and this turns into a second hydranth, soon to give off a third polyp, and so we have the hydrocaulus formed. Simultaneously with this, small processes arise from the attachment disc that grow out and

branch and anastomose in a network, the hydrorhiza, which in its turn serves for the origin of a number of new hydrocauli. In this way there is produced the complex colony, or stock, with which we started.

Before leaving *Obelia* there is one further phenomenon concerning it that calls for notice. Starting with the hydrula we find that by a process of budding, similar to that which in *Hydra* produces a number of separate individuals, there is formed a large colony of hydranths joined by the cœnosarcal canals. It is a matter of opinion whether we regard the whole stock as one individual with the hydranths, blastostyles and medusæ, as separate parts or organs, or look on each of them as an individual in itself, in organic unity with its fellows. The majority of zoologists adopt the latter point of view, and regard the colony as the result of the asexual reproduction of the one person. Further asexual multiplication leads to the formation of the blastostyles, and yet again to the medusæ. The whole colony, together coming from the one hydrula and producing medusæ, forms the asexual generation or **agamobium.** The medusæ, however, do not reproduce by budding, but by the formation of sexually differentiated gametes, and so they constitute the sexual generation or **gamobium.** Thus the life history of *Obelia* includes an asexual generation alternating with a sexual one ; it is an instance of metagenesis or the alternation of generations. It should be noted in passing, however, that such an alternation is not identical with that with which the botanist has to deal in certain plants, *e.g.* the fern. In these plants both the generations produce reproductive cells. The form known as the sporophyte produces single cells, the spores, which are capable of giving rise to an entirely new and different individual without first undergoing any kind of fertilisation. This second form, the gametophyte, cannot produce spores, but only sexual gametes, which must unite to form a zygote before development can proceed any further. Thus we have an alternation of generations often very different in appearance, each capable of giving rise to reproductive cells, a condition which is not paralleled in the animal kingdom. Moreover, among animals, one generation or the other, only rarely both, is capable of vegetative reproduction by budding in a very similar way to *Hydra*.

We have now completed our review of the diploblastic Cœlenterate types *Hydra* and *Obelia*, and have noted in them not only a considerable advance over the Protozoa, but also a certain progressive series of specialisations within the phylum itself, leading to the production of definite localised organs for the performance of certain functions. Thus in these lowly members of the animal kingdom we see indications of the beginning of that complexity of organisation brought about by the physiological division of labour that becomes more and more marked in the higher groups.

CHAPTER VII

THE CŒLOMATA INVERTEBRATA

The Earthworm, *Lumbricus sp.*, a Free-living Annelid—*Tænia solium*, a parasitic flat worm.

THE next grade of animal organisation above the **Cœlenterata** is the **Cœlomata,** and it includes all the remaining animals with a few possible exceptions. The main point of difference between them is that in the latter not only do we find a gut cavity or enteron lined by entoderm, but in addition, between it and the outside layer, the ectoderm, is another cavity, the **cœlom,** whose walls are lined by a third cellular layer, namely, the **mesoderm** or middle layer. Thus there are two independent cavities, enteron and cœlom, and the main structural plan of such an animal reduced to its simplest form is that of a narrow tube, the gut, within a wider one, the body wall, both being joined together at the two ends. In addition to this fundamental difference there are a number of smaller ones which can be better dealt with after we have examined the structure of a primitive cœlomate.

The Earthworm—*Lumbricus sp.,* a Free-living Annelid.

Earthworms are widely distributed over the face of the earth, and are found in almost all places where there is a certain amount of moisture. Of the twenty or more species common in the damp soil of this country the two largest and commonest belong to the Genera *Lumbricus* and *Allolobophora*. They differ from one another only in unimportant points, and for convenience in the laboratory we use the largest of all the British species, namely, *L. herculeus*. They burrow into the ground by literally swallowing the soil in front of them, from which, as it passes through their alimentary canal, they obtain their food, consisting of decaying animal and vegetable matter. It is this earth which is constantly being passed through their bodies, even when upon the surface, that produces the characteristic "worm casts" which spoil the appearance of a lawn or the surface of a putting green. The worm plays a far more important part in the biology of the soil than appears at first sight, and is

invaluable to the plant life. Its burrows allow of the percolation of the rain to the deeper layers, and also of the air. Darwin, in his masterly book on "The Formation of Vegetable Mould through the Action of Earthworms," estimates that by their castings they bring to the surface more than ten tons of the deeper soil per acre per year, and so gradually cover up stones, etc., that may be lying upon it. They also pull in to line their burrows leaves, which, of course, disintegrate, forming a rich mould.

The earthworm's body is long and cylindrical, running off into a bluntly pointed anterior end and a somewhat flattened obtusely truncated posterior end, and its greatest diameter is about one-third of the way from the anterior end. It reaches a maximum length of about seven inches. The general colour is a pinkish-brown, but it is much darker above than below. As it always travels with the same surface to the ground, we can distinguish a ventral and a dorsal surface, the ventral being slightly flatter than the dorsal. Thus it exhibits a definite orientation not only with front and hinder ends, dorsal and ventral surfaces, but also with right and left sides, which are similar to one another, so that it is a bilaterally symmetrical animal.

A series of transverse ring-like grooves divides the body off into about 150 **segments, somites** or **metameres,** which are larger in front than at the hinder end. We also find on dissection that this segmentation is not superficial, but that the inside of the animal exhibits clearly the repetition of the essential organs of the body in compartments of the cœlom, separated off from one another by transverse partitions or septa, which coincide with the grooves on the outside. In its general characters *Lumbricus* agrees with a large number of other worm-like forms, which from their ringed bodies are classed in the Phylum **Annelida** or **Annulata.** This repetition of a number of parts in a series, so very strongly marked in the Annelids, is a morphological feature of considerable importance, and an animal so built up is said to be **metamerically segmented,** while the repeated parts are described as **serially homologous.** It is a feature marked even in the higher animals like the dogfish, and distinct traces of it are still to be found in the frog, rabbit, and ourselves.

At the extreme anterior end of the earthworm is a blunt lobe, the **prostomium**, not homologous with the somites. Behind it, the next part if the worm, the first true somite, surrounds the ventrally situated mouth, and so is termed the **peristomium.** On the dorsal surface a backward prolongation of the prostomium is dovetailed into the peristomium; in Allolobophora the projection extends completely across the peristomium, but in Lumbricus it only goes

about half-way. In the worm the ventral surfaces of segments 8-12 are swollen by the so-called **capsulogen glands,** and on the dorso-lateral aspect of segments 32–37 inclusive in the adult there is a saddle-shaped thickening, the **clitellum** or **cingulum.** The position and appearance of this structure is a useful character for determining the species of the worm, for it varies considerably in different forms, but is constant in the one species. It is functional in secreting a cocoon in which the eggs are laid, and also in furnishing them with a nutritive fluid. The end somite is small and bears terminally the anus, and so is called the anal segment. The outermost layer of cells, the epidermis, does not remain exposed freely, but secretes a very delicate membrane, the **cuticle,** which adheres closely to it. If a dead worm be left some time in water this cuticle can be readily stripped off, and appears as a thin transparent irridiscent sheath. In spite of this covering of smooth cuticle a certain roughness is felt if the ventral surface of the worm is drawn across a finger. Closer inspection reveals the fact that this is due to the presence in the skin of a number of very tiny bristles, the **setæ** or **chætæ.** These are not irregularly distributed, but arranged in four pairs in every segment, save the first and last ; two pairs lie on the ventral surface, and the other two are lateral to these. Each seta has the form of an f-shaped rod of chitin pointed at its ends and thickened in the middle, and is embedded in an invagination of the epidermis, known as the **setigerous sac,** to which are attached certain muscles. They are generally directed backwards, acting as a series of points that help the worm in its crawling, but, when pointed forward, as they can be, make it very hard to remove the worm from its burrow. In the fifteenth segment the two pairs of ventral setæ lying close to the male external aperture are modified to form the **penial setæ.**

Not only do we find a mouth and anus, but a number of other apertures opening to the outside, some unpaired and the others paired. The unpaired openings consist of a number of minute holes in the mid-dorsal line, the **dorsal pores,** lying in the grooves between the somites and leading into the cœlem of the segment in front. They are present in all the grooves save the first seven or eight. The remaining apertures are paired and connected with the excretory or reproductive systems. On every segment of the body, except the first three and the last, are a pair of apertures, the **nephridiopores,** the openings of the excretory organs. They are situated just in front of the outermost seta of the ventral pairs. On the ventral surface of segment 15 are a pair of conspicuous slits with swollen glandular lips ; these are the male apertures, the openings of the vasa deferentia or the **spermiducal pores.** In a

similar position on the segment in front are two small holes, the openings of the female ducts, the **oviducal pores.** Lastly, there are two pairs of minute openings, the **spermathecal pores,** lying in the ventral part of the grooves between segments 9 and 10 and 10 and 11, slightly to each side of the middle line. They open into the spermathecæ, whose function we shall deal with later.

Two of the main features that will at once be seen on opening up an earthworm have already been alluded to, namely, the fact that the alimentary canal is a tube lying in the cœlom, and that the cœlom itself is cut up by a number of septa into separate compartments. The thin muscular septa run from the intersomitic groove to the gut wall, into which they are inserted, causing as a rule a constriction. They are perforated by small holes, so that the various compartments of the cœlom are not absolutely isolated from one another. Septa are absent in at any rate the first two or three somites.

The alimentary canal is a straight tube running from mouth to anus and over the greater part of its course is alike, but at its anterior end it is much modified. As we have seen, the mouth is situated on the ventral side of the first somite, and it leads into a wide thin-walled receptacle, the **buccal cavity,** filling the first two somites. Following this is a large thick-walled, muscular portion of the canal, the **pharynx,** which extends back into the sixth or seventh segment, but is really in front of the septum between 5 and 6. From it radiate out muscular strands, some even piercing the septa behind, by means of which its cavity can be enlarged, and in this way it can act as a suction pump, drawing in anything to which the mouth has been attached. Buccal cavity and pharynx together constitute the first part of the alimentary canal, the **fore gut** or **stomodœum,** and are marked off from the next portion by the fact that they are formed by an ingrowth of ectoderm, whereas the succeeding parts of the gut are derived from the entoderm, an important distinction. The **œsophagus** is a straight narrow tube running back from the end of the pharynx to the fourteenth somite. In the eleventh and twelfth segments three small sac-like swellings, the **œsophageal glands,** are to be found on the sides of the œsophagus. The first pair are actually pouches, **œsophageal pouches,** opening directly into the œsophagus, and the last two pairs are thickenings of its walls, only communicating with it via the pouches. Within, they are divided by partitions into small chambers, and they produce a whitish fluid containing a multitude of small calcareous particles excreted by the large cells which line them, and hence their name calcareous glands. In segments 15 and 16 the alimentary canal is dilated to form a large thin-walled distensible sac, the **crop** or **proventriculus.**

This in its turn is followed by a strong muscular expansion, the **gizzard,** occupying segments 17–19 or 20; but it may project beyond this, carrying the septum with it. It has very strong walls and a chitinous lining, in order to grind up the food before handing it on to the intestine.

The **intestine** itself is a long straight tube extending from

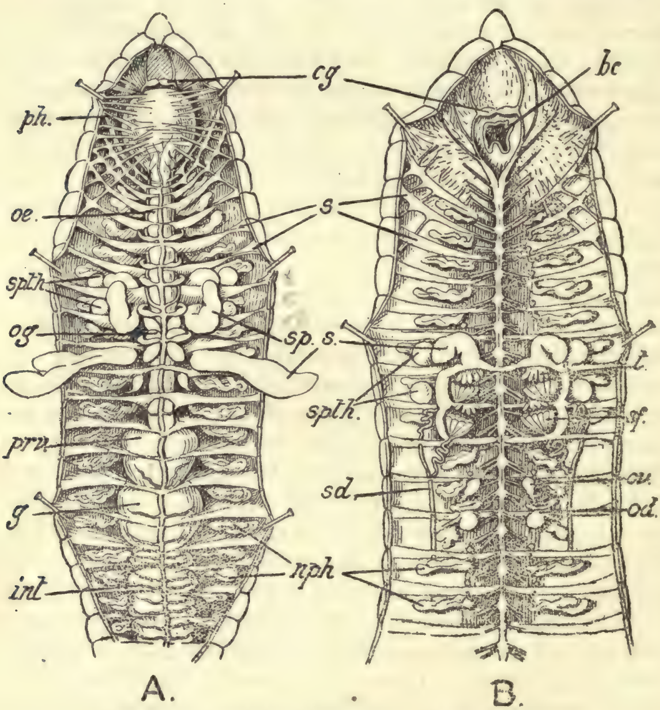


FIG. 55.—*Lumbricus herculeus.*—From Bourne.

A, A view of the organs contained in the first twenty-two somites, as seen when the animal is opened by a longitudinal dorsal incision, and the body walls are pinned out without cutting the septa. The pins are placed in the 3rd, 9th, and 18th somites. B, View of the first sixteen somites of the same worm after removal of the alimentary tract, to show the nervous system and reproductive organs.

b.c., buccal cavity, cut across; *c.g.*, cerebral ganglia; *g.*, gizzard; *int.*, intestine; *nph.*, nephrida; *od.*, oviduct; *oe.*, œsophagus; *ov.*, ovary in somite 13; *ph.*, pharynx with radiating muscular strands; *prv.*, proventiculus; *s.*, septa; *s.d.*, sperm duct; *s.f.*, seminal funnels; *spth.*, spermathecæ in somites 9 and 10; *sp.s.*, sperm sacs; *t.*, testis.

segment 21 to the anus. In each somite it swells up into a sacculation, which is well marked at the anterior end, but diminishes as we pass backwards until it practically disappears at the posterior end, and intersomitically the intestine is contricted where the septa are inserted into it. The sacculations considerably increase the area of the internal surface, an end also served by the dorsal wall

being folded into the cavity to make a very large ridge-like swelling, the **typhlosole,** running the whole way down the intestine. It is lined by entoderm, most of whose cells are ciliated, but there are also scattered in it, particularly on the typhlosole, glandular cells which secrete the digestive fluids. The intestine corresponds functionally to both the stomach and intestine in the higher animals. The outside of it is covered and the interior of the typhlosole is filled with large granular cells of a bright golden yellow colour, causing the intestine to stand out in a striking manner. These **chloragogen cells,** glandular though they are, are not concerned with digestion, but with the excretion of waste nitrogenous matter, as we shall see later.

The earth in front of the worm containing decaying organic matter, its food, is sucked in through the mouth by the action of the pharynx, and is passed on by a series of waves of contraction which travel slowly down the gut one after another, a movement termed **peristalsis.** The earth is thus passed through the œsophagus, where the acids in it are neutralised by the calcium carbonate from the calcareous glands, which may also serve for ridding the body of excess of lime salts. In the gizzard it is ground up, and in the intestine it undergoes most of its digestion and absorption. The proteids are turned into amino-acids, the starches to sugars, and so on, and the soluble products pass by dialysis through the intestinal wall into the adjacent blood-vessels to be distributed to the various parts of the body. The insoluble matter from the food and all the earth is passed out of the anus, forming the "casts" already referred to.

Between the gut wall and body wall the cœlom is filled with a colourless watery matter, the cœlomic fluid, which, as the animal contracts and twists about, is driven backwards and forwards through the perforations in the septa. Thus is set up a very rudimentary circulation which may also help in the conveyance of food, and the fluid may at times exude in tiny drops through the dorsal pores. The plasma of the cœlomic fluid contains two varieties of corpuscles ; in the first place large immobile spherical cells containing many large granules, and in the second typical active amœbocytes with a finely granular protoplasm.

For the first time in the animal series we encounter an animal that has a definite circulatory system and blood ; for such is present in *Lumbricus*, in addition to the moving cœlomic fluid. The blood-vessels are a series of tubes rendered conspicuous by the bright red blood within them. The blood owes its colour to Hœmoglobin, which, however, is not found confined to red corpuscles, as in *Rana*, but is in solution in the plasma. Corpuscles are indeed present,

but they are small flat colourless cells of an elongated oval, almost spindle shape, and comparatively few in number. Circulation is effected by peristaltic contractions of the main trunks, but this is greatly augmented by the action of five, or more rarely six, pairs of enlarged muscular vessels, the so-called hearts. As in vertebrates, the circulation is constant, for the main trunks give off branches which ultimately lead to a capillary network whence the blood is gathered up again by other vessels and returned to the main trunks, thus forming a closed system. In spite of this, however, we cannot employ the terms "arteries" and "veins," as there is no such thing as a central heart, and the vessels are described with reference to the organs they supply ; those bringing blood **to** the organs are **afferent**, and those conveying it **away** again, **efferents.** There are four main series of longitudinal vessels : (1) The **dorsal** or **supra-intestinal** vessel lies in the mid-dorsal line above the alimentary canal, to which it is more or less closely attached, and is the largest trunk in the body. The contractions of its walls drive the blood in it from hinder to front end, and the vessel itself breaks up at both ends into an indefinite series of capillaries. In the region of the intestine this trunk is, as it were, reinforced by another, the **typhlosolar** vessel, which runs near the ventral side of the typhlosole. It is not usually considered as a separate vessel, as it is itself somewhat indefinite, often duplicated, and connected with the supra-intestinal by a large number of anastomosing trunks. (2) The second largest trunk is the **ventral** or **sub-intestinal** vessel situated in the mid-ventral line under the gut, from which it is suspended by a sort of mesentery formed by a fold of tissue. The blood in it passes from before backwards, and at each end it runs into the same capillary plexus as the dorsal vessel. These two trunks, the sub- and supra-intestinal, are placed in direct communication with one another by means of the five pairs of **hearts** which are situated in segments 7–11, and sometimes an additional pair in somite 12. As the blood passes forwards in the dorsal vessel it must flow into and fill the hearts, which by their muscular contraction drive it down into the ventral vessel. The direction of flow anterior to these structures is not obvious. (3) Right on the ventral side of the cœlom lies the nerve cord, and attached to the ventral surface of this is the **sub-neural** vessel, in which the blood flows from before backwards. In the twelfth or thirteenth segment, and all posterior to them, this vessel is directly connected with the dorsal vessel by a **commissural** vessel running laterally around the side wall of the cœlom. (4) The last two longitudinal trunks are a pair of less important ones lying at the side of the nerve cord, and known, therefore, as the **lateral neural** vessels. The dorsal vessel in segment 10 gives off a pair

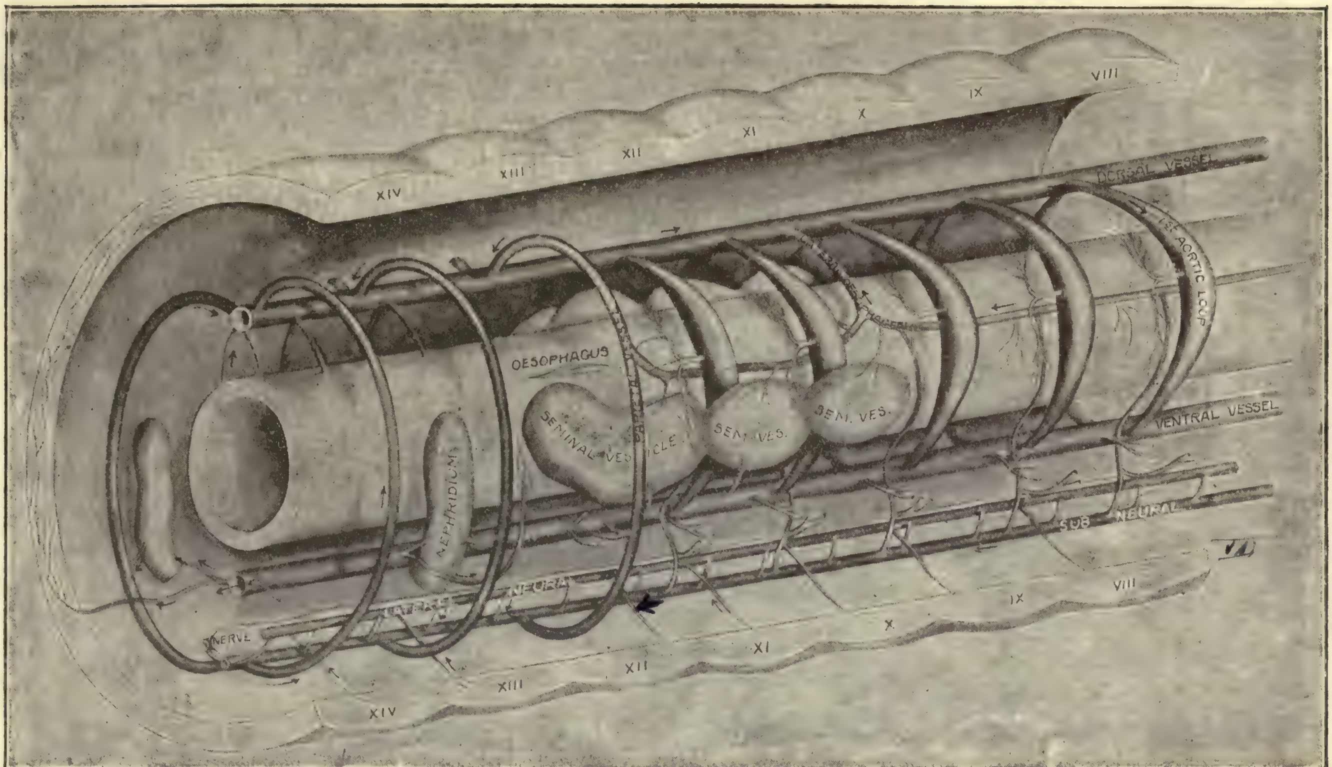


FIG. 56.—Stereogram showing the relation of the circulatory and other organs in the anterior part of the earthworm. (Worked out by Professors McGregor and Calkins, and drawn by Miss Hedge.)

of branches which pass out on to the sides of the œsophagus, and then run forwards into the anterior plexus as the **lateral œsophageal** vessels, and each of these also sends a short branch backwards to flow into the first of the commissural vessels.

The distribution of the branches from these trunks is best considered in relation to the three main capillary circulations that are formed, although the exact details of both the vessels and the direction of the flow of the blood in them is by no means satisfactorily determined. (1) The **intestinal circulation,** which is, of course, mainly concerned with digestion, lies in the intestinal wall. The supra-intestinal trunk gives off two well-marked branches, the **afferent intestinal** vessels, in each somite which run down on the outside of the gut wall. In it they form a rich capillary network, from which the blood is collected up by two **efferent intestinal** vessels in each segment. These convey the food-laden blood along the inner gut wall into the typhlosolar vessel, and this in turn is, as we have seen, closely connected with the dorsal vessel itself. (2 and 3) The next two systems, the **dermal** or **body wall** circulation and the **nephridial** circulation, are closely connected together. From the sub-intestinal trunk in every segment arises a pair of vessels which pass laterally for a short distance and then divide into two. One branch, the **afferent dermal,** goes to the skin, breaking up in the sub-epidermal layers, and the other, the **afferent nephridial,** goes to the nephridium or excretory organ, and both form a very close capillary network. The skin serves as a respiratory organ, neither gills nor lungs being present, and the oxygenated blood is gathered up and returned to the commissural vessel by a series of small **dermal efferents.** In the nephridium the waste nitrogenous matter, and probably also excess of water, is removed from the blood, and thus purified it is collected by one fairly large trunk, the **efferent nephridial vessel,** and this also flows into the commissural vessel.

As has just been indicated, the nitrogenous excretion in *Lumbricus* is carried out by the **nephridia** or **segmental organs.** These consist of a series of complex convoluted tubes arranged metamerically, one pair in each segment of the body save the first three and the last. They lie in the ventro-lateral portions of the cœlom and are closely related to the septa. A small part of each, consisting of a funnel-like opening, the **nephrostome,** projects into a somite from the front of its hinder septum, and hence is known as the **preseptal** portion. This communicates through the septum with the much larger **postseptal** portion, which is a long convoluted tube loosely bound together by connective tissue into three laterally

directed main loops. The nephrostome is situated near the mid-ventral line, from 2–3 mm. from the nerve cord, and the end of the tube comes back to near the middle line, and, running through the body wall, reaches the exterior as the tiny hole, the nephridiopore, whose position has already been pointed out. Thus a nephridium

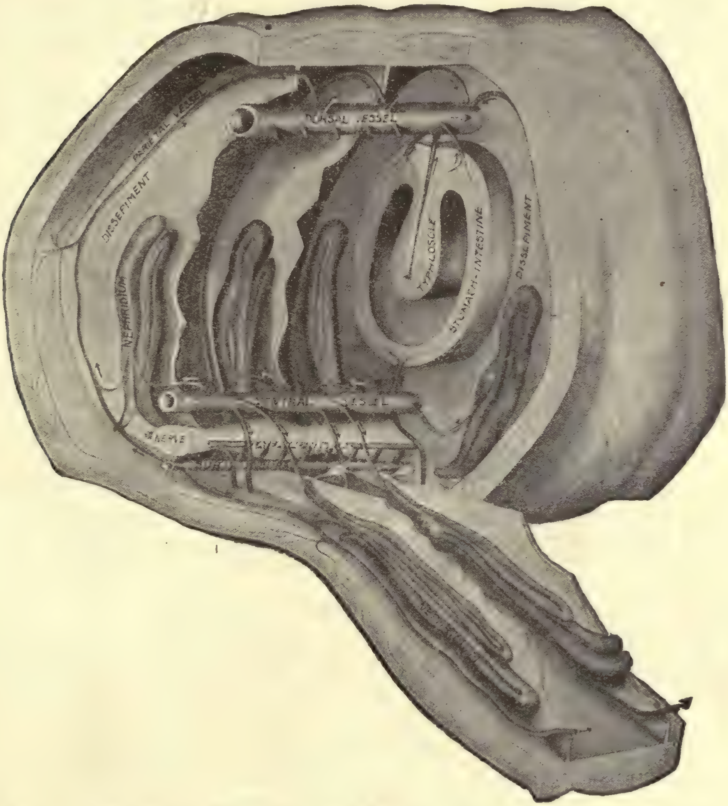


FIG. 57.—Stereogram showing the relations of organs in the posterior part of the earthworm. (Worked out by Professors McGregor and Calkins, and drawn by Miss Hedge.)

opens into the cœlom of one segment, but to the outside through the wall of the following one.

The preseptal part consists of the nephrostome proper and a neck-like portion. The nephrostome is a flat oval kidney-shaped structure, the main part of which is composed of a single large crescent-shaped cell, the central cell. Around the outer margin of this is a row of slightly wedge-shaped columnar cells, the marginal

cells, covered on their dorsal surface with long fine cilia, they are longer in the middle and reduced as they pass towards the side of the crescent. The actual opening is also crescentic, being limited by the central cell ventrally and a projecting lip dorsally. It leads into a narrow ciliated tube, the neck, which after a short distance perforates the septum and passes on into the next part of the nephridium. This tube is surrounded by a sort of collar composed of a syncytium, that is to say, a mass of protoplasm not divided up into discrete cells, but containing a large number of nuclei.

The postseptal, or the main portion of the nephridium, is a very long coiled and looped tube, in which we can easily distinguish four distinct regions. (1) The **narrow tube** is the direct continuation of

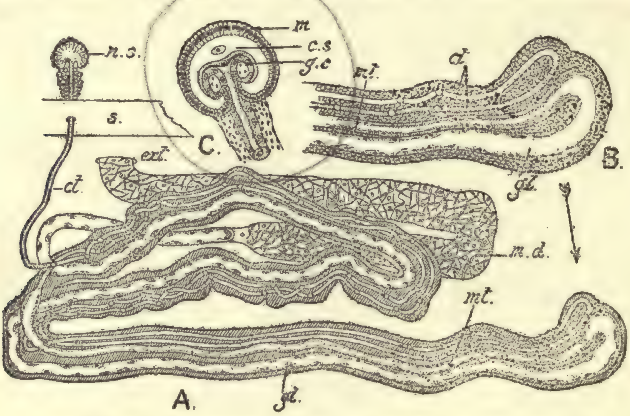


FIG. 58.—A, Diagram of a nephridium of the earthworm.

ns., nephrostome ; *s.*, septum ; *ct.*, narrow ciliated tube ; *m.t.*, middle tube ; *gl.*, wide grandular non-ciliated tube ; *m.d.*, muscular duct. B, a portion of A enlarged to show the passage from the middle tube to the glandular tube. C, a nephrostome enlarged ; *m.*, marginal cells ; *c.s.*, central cell ; *g.c.*, grooved cells. (After Benham.)—From Bourne.

the preseptal tube, and it runs the complete length of the first and second loops returning to its starting-point. It remains narrow throughout, and is much twisted and coiled upon itself, and is ciliated at any rate in parts of its course. At its end it finally leaves the first loop and passes to the inner point of the second loop, becoming transformed as it does so into the next portion. (2) The **ciliated** or **middle tube** is much shorter, starting at the base of the second loop and only running out to its lateral extremity. It is wider than the former, and owes its name to the fact that it is particularly well supplied with long cilia, which remain active and can be seen working vigorously under the microscope for a considerable time after the nephridium has been removed from the body. The walls of this tube are very granular and of a brownish colour.

(3) The succeeding part, the **wide tube,** is still wider than the middle tube, and starts at the distal extremity of the second loop in a distinct vesicular enlargement, the ampulla. This tube also has coloured and very granular walls, for which reason it is sometimes distinguished as the glandular tube. It runs to the base of the second loop and then back through the whole of the first loop to near the point of entry of the narrow tube, where it finally leaves the first loop and passes over into the last part of the nephridium. (4) The terminal portion, constituting the entire third loop, is the **muscular duct** or **bladder.** It opens to the exterior by the nephridiopore, and, unlike the other tubes, has a muscular wall forming a sac, in which the excretory fluid can be stored and ejected to the exterior from time to time. The three loops are bound together by connective tissue, with which is associated a large number of chloragogen cells, and in which is found a capillary plexus that is particularly marked in the portions occupied by the ciliated and glandular tubes.

An important difference is to be noted between the muscular duct and the remaining parts of the nephridial tubes. It is lined by flattened cells, so that its cavity is intercellular, whereas the lumen of all the other portions is intracellular. They are actually composed of a series of hollow cylindrical cells joined end to end, which, from their appearance, are known as drain-pipe cells. This difference is reflected in their development also, the muscular duct arising as a hollow invagination of the ectoderm, while the remaining portion is laid down as a solid strand of ectodermal cells, in which the lumen is formed later.

Excretion in these organs is of a twofold nature. The ciliated and wide tubes are granular in appearance, owing to the presence in them of excretory particles that they have formed by secretion from the blood. These are passed into the lumen and washed down into the bladder by the current set up by the cilia, and so in this way nitrogenous waste and water are eliminated. The other kind of excretion is possible, owing to the fact that the nephrostome opens directly into the cœlomic fluid, and the cilia covering the marginal cells work in such a way as to convey any small particles to its opening, which is, however, too small to allow of the passage of amœbocytes. Any foreign bodies, bacteria, etc., that may have entered through the dorsal pores can be removed in this way. The main bulk of the matter removed by this channel, however, is derived from the chloragogen cells. These gradually secrete within themselves granules of excrement, and when full come loose from the gut wall into the cœlomic fluid. Here they break down into tiny fragments, which are gradually swept down the nephrostome by the action of the cilia. The amœbocytes also

appear to play an active part in this process, by collecting up the various granules and conveying them to the nephrostome, where they yield them up again. It is considered by some authorities that this excretory function on the part of the peritoneal cells is a primitive one, and was the sole one before the evolution of the special and complex segmental organs, the nephridia.

The **muscular system in the worm** is a very simple one, consisting in the main of two double sheaths of muscle fibres. The first is the somatic or body wall musculature, and it consists of a series of muscle fibres arranged circularly all along the animal underneath the epidermis, save where it is interrupted intersomitically at the grooves, and a much thicker layer of longitudinal muscles. The latter are bounded internally by the lining of the body cavity, the peritoneum, and are arranged in bands. Two dorso-lateral bands extend from the mid-dorsal line, where they are just separated from one another in the line of the dorsal pores, to the line of the lateral setæ, whose enveloping sacs again form a break. The two latero-ventral bands occupy the spaces between the lines of lateral and ventro-lateral setæ, and, lastly, a ventral band occupies the mid-ventral line. The tiny longitudinal muscle fibres are arranged on each side of a large number of radially-running partitions, and exhibit in transverse section a very characteristic feather-like appearance. The second sheath is the splanchnic or gut wall musculature, and it consists of an inner very thin layer of circularly arranged fibres lying beneath the entoderm and an outer even thinner layer of longitudinal fibres. These two layers are considerably developed in the pharynx and gizzard. They are bounded by the splanchnic or gut layer of peritoneum, whose cells are highly modified in the intestinal region to form the chloragogen cells. In addition to these sheaths there are the special muscle strands already mentioned as radiating from the pharynx. All the muscles seem to be composed of cellular non-striated fibres.

The normal method of **reproduction** takes place sexually by the production of gametes, but if a worm is cut up into a number of pieces, each, as in *Hydra*, possesses the power of regeneration, enabling it to regrow the lost parts. Thus the agriculturist who viciously cuts a worm in halves with his spade is doing his land more good than he knows, not by removing a worm, but by adding to their numbers. *Lumbricus* is **monœcious** or **hermaphrodite,** the two essential sexual organs, ovaries and testes, occurring in the

same individual. In spite of this, however, it is unable to fertilise its own ova, and cross-fertilisation by another worn is brought about in a manner we shall discuss shortly. The reproductive organs lie towards the anterior end, and are included in segments 9–15.

The most conspicuous parts of the reproductive organs are large white sac-like structures, lying ventrally and laterally to the œsophagus, apparently in segments 9–12 or 13. These are the **sperm reservoirs,** or **vesiculæ seminales,** in which are to be found spermatozoa in all stages of development, and although they vary in size at different periods of the year they are always readily made out. They consist of two mesial sacs, the anterior and posterior median sperm sacs, situated in segments 10 and 11 respectively. From the front corners of the former arise a pair of antero-lateral sperm sacs, which push forward in front of them the septum between segments 9 and 10, and so appear to lie in somite 9. The hinder corners in a similar way give off the median lateral sperm sacs, which push back the septum between 10 and 11, and so seem to lie in segment 11. The postero-lateral sperm sacs come off from the caudal corners of the posterior median reservoir, and although really lying in somite 11 project backwards into segment 12 and often 13, carrying the septum between 11 and 12 with them. They are very large structures. In almost any part of the vesiculæ seminales there may be living *Monocystis agilis,* the protozoon parasite already studied, which may be found by examining a smear of their contents under the microscope. The actual male reproductive organs are difficult to see, as they lie within the sperm sacs, and the dorsal wall of these structures must first be removed. There are two pairs of testes, one pair in each of segments 10 and 11. They are small flattened digitate bodies, attached to the hinder surfaces of the septa between somites 9 and 10, 10 and 11, and projecting freely into the cavity of the sperm sacs. Each is formed by a localised thickening of the cœlomic epithelium covering the septum, and is composed of a mass of cells, the **spermatogonia** or sperm mother cells. The spermatozoa are not actually produced in the testes, which only shed into the sperm sac small groups of from eight to sixteen spermatogonia, and there these are transformed into sperms. On the anterior faces of the other septa in the same somites and opposite to the testes are four fairly large funnel-shaped apertures, which from the complexly folded nature of their margins are known as the **"ciliated rosettes."** It is to these structures that the large parasite *Monocystis magna* is to be found attached; it does not float freely, as does its smaller relative *M. agilis*. These funnels lead through the septa into very fine convoluted tubes, the **vasa efferentia,** which unite towards the posterior end of the twelfth segment to form the single **vas deferens** on each

side of the body. This fine duct passes straight back on the ventral floor of the cœlom to somite 15, where it passes through the body wall to the external male aperture.

The female part of the reproductive system is much less conspicuous than the male. Only one pair of ovaries is present, situated on the hinder surface of the septum between segments 12 and 13, and projecting freely into the cavity of the latter. The ovary is again a localised thickening of the cœlomic epithelium, forming a pear-shaped body about 2 mm. in length. At the anterior wider end is a mass of small cells, the **primordial ova** and the **oogonia,** and the narrower end is formed by a single row of large nearly ripe ova, each surrounded by an envelope of thin cells constituting a follicle. Two short ciliated funnel-shaped openings, the **oviducal funnels,** are situated on the septum at the opposite end of the somite vis-à-vis to the ovaries. They perforate the septum as oviducts, and immediately on the posterior side of it each undergoes an enlargement to form a small sac, the **receptaculum ovorum** or **ovisac.** After a very short straight course the oviducts open to the outside in segment 14.

In addition to these sets of male and female organs we also find four accessory structures, the **spermathecæ,** whose function we shall discuss shortly. These are two pairs of ovoid whitish or light yellow sacs, lying ventro-laterally in the posterior halves of somites 9 and 10.

The testis, as has been noted, sheds masses of protoplasm with from eight to sixteen nuclei, but only indistinctly divided into cells, the spermatogonia. In the vesiculæ seminales these apparently undergo two successive divisions, producing 32 to 64 much smaller cells, the spermatids, around a central mass of protoplasm known as the **cytophore.** These cells gradually alter until they form very typical spermatozoa with small heads and long filiform tails, which still retain a spherical arrangement around the central mass. These groups of cells exhibit a very characteristic mulberry-like appearance during these changes, and are in consequence known as the sperm morulæ. Finally, the ripe sperms are set free into the fluid content of the sperm sacs. It is into the cytophore of the spermatozonia that the young sporozoite of *M. agilis* bores its way and gradually consumes it while the surrounding spermatozoa are undergoing their maturation divisions. The tail of the ovary, as we have seen, contains a string of large nearly ripe ova each enclosed in a follicle, which presently bursts releasing the ovum, which is taken up by the oviducal funnel and stored in the receptaculum. Here it undergoes further ripening until it becomes mature.

During the act of copulation two worms lie together in head

to tail directions in such a way that the opening of the vasa deferentia of the one come to lie opposite to the openings of the spermathecæ in the other and vice versa. The sperms are then transferred from each worm to the spermathecæ of the other, where they can live for some time until required, after this the worms separate. It is these spermatozoa that fertilise the ova of the worm in which they are lodged, and consequently the ova of one worm are cross-fertilised by the sperms obtained from another. Some time after copulation the clitellum secretes freely a substance which as it hardens forms an elastic band, the cocoon, round the worm and at the same time it also secretes into it a nutrient fluid. The worm then wriggles backwards in this, and when it comes to lie opposite to the oviducal pore the eggs from the receptaculum are laid in it, so that it can also be spoken of as an egg capsule. Further wriggling brings it over the spermathecal pores, and here the sperms are discharged and fertilisation takes place, one sperm entering each ovum. A supply of albuminous fluid is added to the contents of the cocoon to serve as food, and finally the worm completely escapes from it and it automatically closes at its two ends by its own elasticity. The cocoon when left behind in the earth is a toughish oval sac of yellow or yellowish-brown colour about 5 or 6 mm. in length. Although a large number of eggs are laid and even fertilised, only a few or perhaps even one alone undergoes complete development. The nutritive fluid serves as food for the growing embryo, which when it leaves the cocoon is already a minute little worm but quite complete, and it only needs to grow in order to become a mature adult. Thus we have no free living larval stage to correspond with the planula of *Hydra*, and the development is direct from an egg through an embryo to the definitive adult form.

As in the frog, the nervous system of Lumbricus may be divided for convenience of description into a central and a peripheral portion, and so represents a condition considerably in advance of that in *Hydra*, for it is a concentrated and not a diffuse system. On the internal side of the ventral body wall in the middle line the nerve cord is to be seen as a long whitish cord exhibiting an enlargement or ganglionic swelling in each segment of the body. In the fourth somite the swellings are quite marked, forming the **sub-pharyngeal ganglia,** which diverge from one another and are continued forward around the pharynx as two moderately fine nervous strands, the **circum-pharyngeal connectives.** These pass on to the dorsal side of the alimentary canal and terminate in the third somite in two conspicuous enlargements touching one another in the middle line, the so-called **cerebral** or **supra-pharyngeal ganglia.** Although appearing as a single strand the ventral cord is, morphologically

speaking, two cords running side by side and joined by transverse bands, the commissures, and this structure becomes more apparent when viewed in transverse section. It arises also as two distinct cords on the ectoderm of the embryo, which become approximated as they sink in from the outside, and it is to be regarded as a modification of a type of nervous system quite common in invertebrate animals. This sort of nervous system consists typically of two parallel ventrally situated lines of ganglia linked on each side by longitudinally running connectives and joined by a transverse commissure joining the two ganglia in each segment. From its characteristic appearance this sort of nervous system is termed the rope-ladder type. It is masked in the worm by the apposition of the two cords and the shortening of the commissures transversely, but extension of them longitudinally. Running in the groove on the dorsal side of the cord are three long fibres, the giant fibres, containing the axons of certain large ganglion cells, and these, together with the cord itself, the ventral neural and lateral neural vessels, are all bound together by one fairly tough fibrous connective tissue sheath.

The peripheral nervous system is composed of the nerves and the sensory cells situated in the epidermis. A series of paired nerves come off from the central nervous system and are distributed generally to the viscera and body wall. The first pair arise from the front end of the cerebral ganglia and pass forwards to supply the prostomium, being apparently mainly sensory in function. A second pair start from the circum-pharyngeal connectives and supply the peristomium. The third pair are large and run forward from the sub-pharyngeal ganglia to be distributed partly to the peristome, but mainly to the second and third somites. In each of the remaining segments there are typically three pairs of nerves ; two pairs come off close together from the ganglion in the mid somitic region, and the last pair, originating in the connectives at the front end of each somite, are distributed mainly to the septum just behind which they arise. The sensory cells are present in the epidermis, occurring singly or in groups, forming the so-called sense-buds. A large number of these are present, particularly at the anterior end of the animal. They lie among the ordinary epidermal cells and are arranged in rings, of which there may be three in each somite, the middle one containing as many as sixty buds.

The mass of the central nervous system is composed of ganglion cells and their processes, and they are in the main of two sorts, although a third variety, a sensory ganglion cell, may also be present. 1. The **motor neurons** are typical nerve cells, mainly pear-shaped and bipolar but sometimes multipolar, whose dendrons are situated within the ventral cord. They are more numerous in

the ganglionic enlargements than in the connectives, although they are also present in these. Their axon leaves the cord as a non-e? medullated afferent or motor nerve fibre, and runs outwards, frequently terminating in a muscle. They may, however be acceleratory, inhibitory, or excitatory in function when they are distributed to other parts than the actual muscle elements. 2. The **commissural** or **association neurons** are only to be found in the cord itself and are bipolar. The axon and single dendron are very similar to look at, and they function in placing the various other nerve elements in communication with one another. A sense-bud, which causes a slight projection on the surface of the epidermis, is composed of a number of elongated rod-like sensory cells. Each cell bears at its

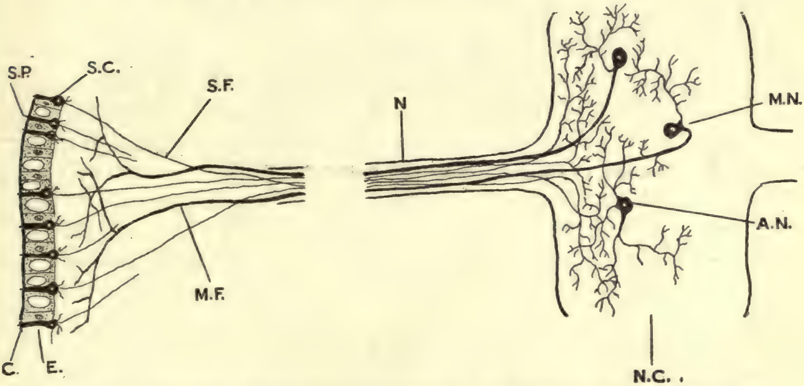


FIG. 59.—Diagram to show the relations of the nerve cells in *Lumbricus*, adapted and modified from Lenhossek and Retzius.

A.N., association neuron ; C., cuticle ; E., epidermis ; M.F., motor fibre ; M.N., motor neuron ; N., nerve ; N.C., nerve cord ; S.C., sensory cell or sensory neuron ; S.F., sensory fibre ; S.P., sensory process.

external end a short stiff sensory or receptive process, and the cuticle overlying it is pierced with a small hole to allow it to project freely to the exterior. At its inner end the sensory cell is continued on as an afferent or sensory fibre, whose terminal dendrite arborises in connection with the association neurons. The whole structure is a typical neuro-epithelial cell, whose receptive process corresponds with the dendron and the fibre with the axon, and is comparable with the olfactory cell in the frog. It is also probable that certain sensory neurons are to be found in the cord, and in this case their dendrons, which terminate by branching round a modified epidermal cell, would form the afferent fibre, but such cells are apparently not very numerous. Through these various sensory cells the earthworm is put in communication with the outer world, and so can appreciate

sensations of touch, taste, smell and light, but so far as we can ascertain it is incapable of receiving sound impressions. The sense of touch is the most widely distributed of them, and is spread all over the body. Next to that is the sense of light, which is present all over the anterior end but is absent from the posterior half of the worm. The senses of taste and smell are more limited in their extent, being confined almost entirely to the prostomium, the peristomium near the mouth, buccal cavity and pharynx.

Let us now consider the mode of action of the nervous system as a whole. Four elements are involved in the reflex arc in the case of the worm, three of them are nervous and the other a muscle. The sensory receptor projecting from the epidermis with its afferent process arborising in the cord is in connection with the dendron of an association neuron, and the axon of this cell is in turn related to the dendron of a motor cell. Thus the stimulus is transferred from the skin to a motor neuron, and thence sent down, via its axon, to the muscle connected with the epidermis, bringing about a movement of the latter. This then is a very simple reflex arc, and although quite a small stimulus is bound to affect a large number of sensory cells and an even larger number of motor neurons the process is essentially the same. The cerebral ganglia certainly play a part in co-ordinating the movements of the animal as a whole, but not to nearly such a large extent as does the brain of the frog, and the main activities of the worm are the result of these reflex actions. This is most clearly seen when a worm is cut to pieces, for each part, although entirely removed from any connection with the cerebral ganglia, still exhibit normal movements, which must of necessity be reflexes, and the ganglion pair in each somite is the centre of such actions for its own segment. The presence of the commissural neurons with their well-branched axon and dendron makes it possible for a sensory impulse, even coming from a limited area, if sufficiently strong, to be distributed to a fairly large number of motor cells, and consequently to bring about adjusting movements on the part of larger portions of the body or even of the animal as a whole. By these means, then, the movements of the worm in response to the stimuli produced by changes in its environment are brought about.

An examination of a transverse section of *Lumbricus* when compared with one of *Hydra* will reveal certain of the important differences, not merely between the animals themselves, but between the Cœlomata and Cœlenterata. In *Hydra*, as we have seen, the body wall is simple, consisting of an ectoderm and an entoderm with the intermediate mesoglea, and it bounds a single internal cavity, the cœlenteron. In *Lumbricus* the body wall is composed of five distinct layers. 1. The cuticle is the outermost, and consists

of a thin transparent membrane, composed of two sets of intercrossing fibres perforated by fine pores. 2. The ectoderm or epidermis below the cuticle is composed of short columnar cells, forming a simple epithelium, and containing a large number of mucous secreting gland cells, and also the sensory cells arranged singly or in groups. In the region of the clitellum the epidermal cells are greatly enlarged and mostly glandular. The blood capillaries actually penetrate this modified part of the epithelium—a very unusual

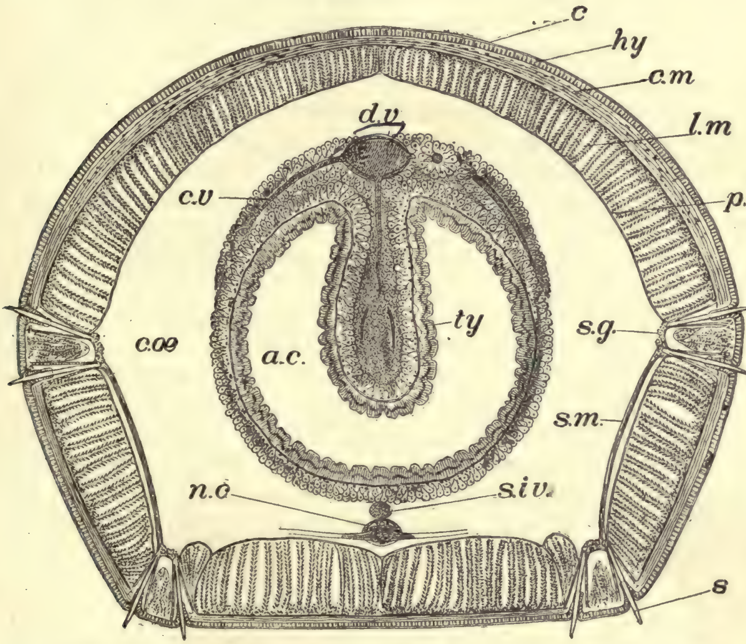


FIG. 60.—Transverse section of the earthworm behind the clitellum.

a.c., cavity of the digestive tract; *c.*, cuticle; *cœ.*, cœlom; *c.m.*, circular muscles; *c.v.*, circular vessel; *d.v.*, dorsal vessel; *hy.*, hypodermis; *l.m.*, longitudinal muscles; *n.c.*, ventral nerve chain; *p.e.*, peritoneal endothelium; *s.*, seta; *s.g.*, setigerous gland; *s.i.v.*, sub-intestinal vessel; *s.m.*, muscle connecting two groups of setæ on the same side; *ty.*, typhlososle.—From Sedgwick and Wilson.

occurrence in the animal kingdom. Certain insinkings of the epidermis form the setigerous sacs, in which the setæ are lodged. Each is the product of one cell, and as the setæ are constantly being worn out and replaced there are always setæ to be found within the sac in various stages of development. They lie in a group of active glandular cells which surround the bases of the two sacs in each pair, and these masses constitute the setigerous glands. 3. Next to the epidermis we find a moderately thin layer of circular muscle fibres,

in which is a rich capillary network. They are embedded in a matrix of connective tissue, which is pigmented on the dorsal side. The muscle fibres themselves consist of long narrow-pointed cells, each with a nucleus situated in a central core of unmodified protoplasm surrounded by a layer of finely striated contractile material. 4. These are followed by a much thicker layer of longitudinal muscle fibres. They are also embedded in connective tissue and arranged in a very characteristic manner on both sides of fine radially disposed partitions. 5. Lastly, we find a thin layer of very flattened cells forming the somatic part of the cœlomic or peritoneal epithelium. Within this complex body wall is a large space, the body cavity or cœlom, in which lie the gut, the blood-vessels, the excretory organs, etc., and which is not represented in any way in *Hydra*.

The wall of the gut is also complex, being composed of four layers. 1. Lining the inside of the alimentary canal is a single layer of long columnar epithelial cells, most of which are ciliated, but quite a fair number are glandular. They are over the greater part of its length entodermal, and constitute the enteric epithelium. 2. Outside this is a thin layer of circular muscle fibres, by means of which the peristaltic movements of the alimentary canal are produced. They are also supplied on their inner side by the rich sub-epithelial capillary plexus, which plays a large part in the activities concerned with digestion. 3. A very thin layer of longitudinal muscle fibres surround the circular ones. 4. Lastly, these in their turn are covered by the visceral or splanchnic part of the peritoneal epithelium. In the intestinal region the cells of this layer are transformed into the striking chlorogogen cells, whose appearance and structure has already been dealt with.

Thus in *Lumbricus* between the ectoderm and entoderm there is a well-developed third cellular layer, the mesoderm, complexly differentiated into muscles and epithelium, and divided into a somatic portion, forming the main part of the body wall, and a splanchnic part, helping to build up the gut wall, and between these two is the large cœlom. This cavity exhibits the three main characteristics of any true cœlom; it is lined by mesoderm and surrounds the gut, the gonads are produced by its epithelial lining, and the primitive excretory tubules open into it. Such a type of structure is quite characteristic of all the higher Cœlomata, although in some groups it may become secondarily modified.

Further differences are to be noted between *Hydra* and *Lumbricus*. The latter form has a well-developed muscular system composed of muscle fibres and not of epithelio-muscular cells. The alimentary

canal is far more highly developed, and possesses two external openings, a mouth and an anus, and in addition sac-like glandular outgrowths. It can be divided into an anterior part lined with ectoderm, the stomodœum, a mid portion lined with entoderm, the midgut or mesenteron, and a very small posterior portion also lined with ectoderm, the proctodœum. Owing to the presence of the cœlom many parts of the body are separated from the alimentary canal, and this is itself removed from the oxygen of the air, and so we find a well-developed circulatory system for the distribution of nutriment and for respiration. The gonads are inside the cœlom of the worm, and consequently require genital ducts to convey their products to the exterior. In *Hydra* both layers form a free surface over which excretion can take place, but many layers in *Lumbricus* are not free, so that it possesses a series of complex excretory organs for its nitrogenous waste in the form of segmentally arranged nephridia. Lastly, the diffuse network of nerve cells in *Hydra* is replaced by a compact ventrally situated central nervous system, connected on the one hand with the muscles, and on the other with a number of sensory cells in the ectoderm. All of these points are also characteristic of the higher cœlomates, save that in the Vertebrata the concentrated nervous system is on the dorsal side of the animal; and although in the early development the excretory tubules are segmentally placed, they lose this primitive arrangement in the adult. Thus, just as *Hydra* represented a considerable advance on the Protozoa, so *Lumbricus* in its turn is on a much higher plane than the Cœlenterata, and, indeed, its metamerism and general plan, although sometimes much modified, and to be traced throughout all the higher animals.

Turning now to consider the development of *Lumbricus*, it is, as might be expected, much more complicated than that of *Hydra*, and we need only take notice of its main features. The egg is laid, as we have seen, with others in a cocoon provided with a store of nutrient fluid, and is spherical and fairly transparent, with a relatively small amount of yolk. The segmentation or cleavage of the egg is complete or **holoblastic,** that is to say, the lines of division cut the original ovum up completely into separate cells, and a hollow sphere of cells or blastula is formed. The cells of the blastula are of unequal size, being divided into an upper set of small ones, the **micromeres,** and a lower set much larger, the **macromeres.** All the cells continue to divide, getting smaller in the process, save two neighbouring macromeres near the equatorial line. These remain of large size, and as they are destined to give origin to the mesoderm are variously

known as the **teloblasts, pole cells** or **primary mesoderm cells.** The blastula now commences to alter in shape, and from being spherical gradually becomes elongated and flattened, till it forms a flattish

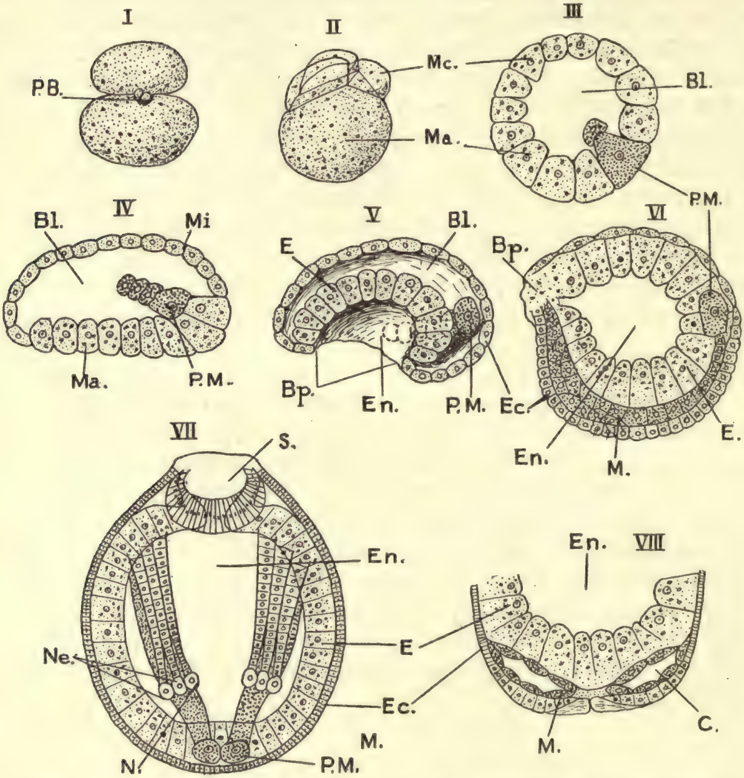


FIG. 61.—Diagrams of the development of *Lumbricus*, mainly adapted from Wilson.

I. and II., early segmentation stages ; III., section through the blastula showing the primary mesoderm cell which has divided ; IV., section of beginning of invagination, macromeres forming a flat plate, more mesoderm cells formed ; V., view of half an embryo during invagination ; VI., section through gastrula after obliteration of blastocœl and closure of blastopore ; VII., ventral view of embryo at a later stage showing stomodœum and germ bands ; VIII., transverse section of lower part of an embryo showing the cœlom arising as a split in the mesoderm.

Bl., blastocœl ; Bp., blastopore ; C., cœlom ; E., entoderm ; Ec., ectoderm ; En., enteron ; M., mesoderm ; Ma., macromeres ; Mi., Micromeres ; N., cells giving rise to nerve bands ; Ne., cells giving rise to nephridial bands ; P.B., polar bodies ; P.M., primary mesoderm cells ; S., stomodœum.

oval cake, the small cells on the upper surface and the large ones on the flat under face. Simultaneously with this alteration in shape the teloblasts have sunk more and more into the embryo, until they pass right into the blastocœl, and at the same time they have each undergone a series of unequal divisions. These divisions result in

the production of two internally situated rows of cells, the mesoderm bands, passing forwards from the posteriorly situated original pole cells. This process goes on for a long time, and in its early stages considerably reduces the blastocœl cavity. Thus we have a hollow embryo with an upper layer of small cells, a lower layer of large cells, and intermediate lines of cells, the primary mesoderm.

After this, gastrulation, the conversion of the blastula into a gastrula by the formation of the entoderm and enteron, takes place. The lower larger cells invaginate, causing the edges of the cake tc turn in and at the same time the upper cells gradully grow over more and more. Thus is formed an oval still somewhat flattened structure covered with smaller cells, the ectoderm, and having on the ventral surface a large oval aperture, the blastopore, which leads into the archenteron or primitive gut, whose walls are formed of the large cells, the entoderm. In this way we have laid down the three layers characteristic of the adult cœlomate, the ectoderm, entoderm, and mesoderm.

The embryo grows slowly in length and simultaneously the blastopore gets narrower, ultimately closing up from the posterior end forward, leaving only a tiny round opening at the front, which persists and marks the place where the ectoderm will grow inwards to form the stomodœum. As soon as this last structure has made its appearance the embryo is able to swallow the nutritive fluid contained in the cocoon, and this causes the archenteron to swell until it touches the ectoderm save in the regions occupied by the mesodermal bands, thus obliterating the blastocœl.

With further growth noticeable changes take place in these rows of cells, which with the closure of the blastopore come to lie quite near together close to the mid-ventral line. Not only do these bands increase in length by transverse divisions, but at the front end they also become wider, and instead of consisting of only one cell they are transformed by longitudinal divisions firstly into bands of two or three cells deep. Subsequently they become wider and wider, and at the same time each band is cut up at its anterior end into a series of masses which form a series of paired blocks on each side of the middle line, the **mesodermal somites.** They are at first small and solid, but a cavity, the cœlom, appears in them, and they increase fairly rapidly in size and grow upwards between the ectoderm and entoderm so as to surround the gut. Finally, they meet dorsally to the archenteron, and then their cavities run into one another above and below, so that the mesoderm is divided into two parts, one surrounding the gut and the other lining the ectoderm. In this way we have established a body wall composed of ectoderm and a layer of mesoderm, constituting the **somatopleure,** and a gut wall or **splanchnopleure,**

formed of the entoderm and inner layer of mesoderm. The double transverse walls of the somites become approximated and persist as the septa, and a groove is formed in the ectoderm outside. This forms the intersomitic groove, so that the animal becomes ringed, and the segmentation which was first laid down in the mesodermal bands is visible externally.

By this time the embryo as a whole has become considerably elongated and distinctly wormlike in appearance, and the subsequent course of its development need not be noticed in detail. The ectoderm gives rise to the epidermis of the adult, which in its turn secretes the cuticle and the setæ. At a somewhat earlier period, even before the cœlom surrounds the gut, a line of modified cells appears in the ectoderm on each side of the mid ventral line, and this later sinks into the cœlom and produces the ventral nerve cord. Immediately lateral to these lines are two other longitudinal rows of special cells, which are similarly passed into the cœlom, and these are the primordia or beginnings of the nephridial tubes. Gonads and genital ducts appear to be derived from the mesoblast. The somatic mesoderm supplies the muscles and blood vessels of the body wall and the outer layer of cœlomic epithelium. The muscles, blood-vessels and covering epithelium of the gut wall are derived from the splanchnic mesoderm. The entoderm forms the main part of the gut lining of the adult, but is supplemented by an anterior invagination of ectoderm, the stomodœum, and a much smaller posterior ectodermal invagination, the prœtodœum, which forms the anus.

As growth proceeds new somites are added at the posterior end, just in front of the original teloblasts, which therefore mark the growing point of the worm. The first of the mesodermal somites to be laid down is the one surrounding and partly behind the mouth, *i.e.* the peristomium, and thus we see that while the whole of the remaining parts of the worm is developed in connection with the somites and is metamerically segmented, there remains the small portion in front of the mouth, anterior to the old blastopore, which never forms part of this series. This is the prostomium. The adult worm furnishes a splendid example of serial homology in the metameric repetition of its parts.

From the free-living cœlomate *Lumbricus* we now pass on to consider another quite different and more degenerate type of worm which is parasitic and only distantly related to *Lumbricus*.

Tœnia solium, a parasitic flat worm.

Tœnia solium is the tapeworm that is commonly found living parasitically in the intestine of man in European countries.

The body has the form of a long narrow ribbon, well deserving its name of "tape" worm, and may reach a length of many feet or yards; one is recorded as attaining the enormous length of thirty metres. At the front end is a tiny knob-like swelling, the head, by which the animal attaches itself to the wall of the alimentary canal, and this is followed by a very thin thread-like unsegmented portion, the neck, and the head and neck together constitute the **scolex.** This part is usually missing in laboratory specimens, and is so small that it would be readily overlooked. At the posterior end of the neck are indistinct transverse grooves, which become more and more distinct as we pass backwards, soon dividing the body up into a series of discrete segments or better **proglottides,** which constitute the genital part of the animal, the **strobilla.** The proglottids have the form of narrow transversely placed rectangles, but farther back they are longer, forming almost square sections and then longitudinally running rectangles. The main part of the body is then composed of a series of segments, and so presents a superficial resemblance to a segmented Annelid, but they are not truly typical metameres or somites. Each contains little more than a complete set of reproductive organs, which are immature at the front end. When fully formed the proglottids are termed mature, and at the hinder end, where they are almost filled up with a much branched uterus laden with eggs, they are said to be ripe. In this condition they are fated to drop off from the end of the chain either singly or in groups, and passing to the outside with the fæces of the host bring about the dissemination of the species. So it comes about that the ripe proglottids are shed from the end of the series, new ones are formed just behind the neck, which is therefore the growing point, and the host is not free of the pest, however many proglottids are removed, as long as the scolex remains behind, and this is always difficult to dislodge.

The head is the organ of attachment, and for this end is furnished with clinging organs in the form of suckers and hooks. The suckers in *T. solium* are oval, cup-shaped, strongly muscular structures situated on the head, to which they give a rough rectangular shape. In front of the suckers is a broad conical projection, the **rostellum,** furnished with a double row of strong chitinous spines. This is capable of being protruded and retracted. The number and shape of the suckers and presence or absence of a rostellum or its spines form important characters, by means of which the various species of tapeworm may be distinguished.

Living as it does in the alimentary canal, it is surrounded by food in a diffusable condition, and as a result we find it devoid of a mouth, a gut, or any form of digestive system, feeding taking place by

diffusion. The nervous system is quite simple, and consists of two well-marked ganglia in the head connected together by a transversely placed commissure. From each of the ganglia a fine nerve cord runs backwards along the lateral border of the proglottids. The most conspicuous parts of the excretory system are two longitudinal canals running just inside the lateral nerve through the whole

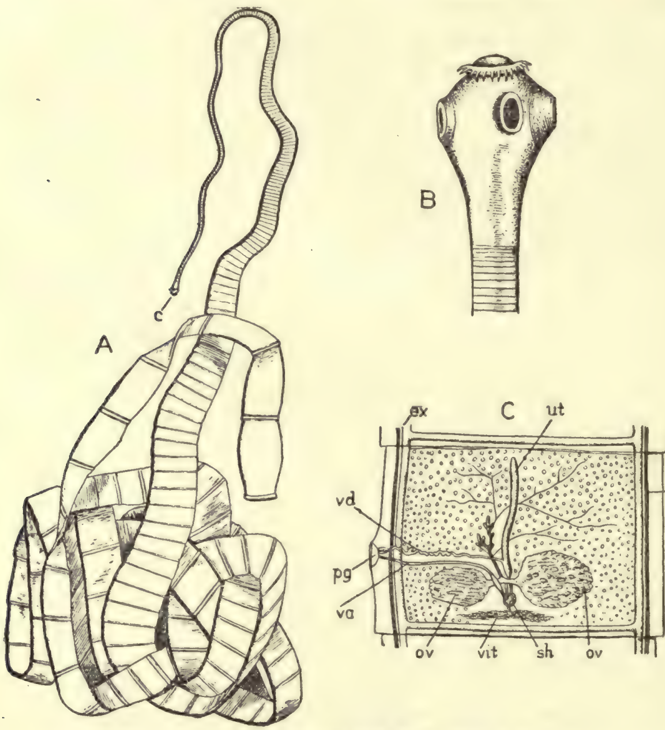


FIG. 62.—Tapeworm of the pig, *Tænia solium.*

A., entire specimen, reduced ; *c.*, head ; B., head or scolex, showing adhesive hooks and suckers' enlarged ; C., proglottid or segment, enlarged, with mature reproductive apparatus ; *ex.*, excretory canal ; *n.*, longitudinal nerves ; *ov.*, ovary ; *pg.*, genital pore ; *sh.*, shell gland ; *ut.*, uterus ; *va.*, vagina ; *vd.*, vas deferens ; *vit.*, vitteline gland. (After Leuckart, from Parker and Haswell.)—From Lull.

length of the strobilla, and therefore opening at the hinder end of the last proglottid. They are connected at the posterior end of each proglottid by a transverse canal, and receive a rich network of very fine vessels, ramifying all through the tissues of the tapeworm and terminating in branches which end blindly in highly specialised cells. These cells form a pear-shaped hollow and give off a few very long cilia, which hang down into the tubule and execute constant

waving movements, which give to the group as a whole a curious flickering movement, recalling a candle flame in a slight draught, and hence they are termed "flame cells." They are the characteristic excretory organs of the class of flat worms to which *Tœnia* belongs, and the lumen of the tubules at the end of which they occur is intracellular.

A transverse section shows that the proglottid is solid and covered by a cuticle, which is secreted by a layer of modified sub-cuticular cells. These represent a transformed epidermis, which has come to be partly embedded in the underlying tissue. The whole of the interior not occupied by definite organs is filled up with very characteristic cellular padding tissue, the parenchyma. This is a mesodermal product, and although a large cœlom like that in *Lumbricus* is never developed, we still classify them as cœlomates, mainly on account of the development of the mesoderm. A few scattered cells in the parenchyma secrete small calcareous particles, which are of a spherical or oval shape. The muscular system is only feebly developed, as there is but little need for movement, and it consists of a thin dermal layer and a deeper layer made up of thin sheets running in transverse and oblique directions, some forming strands passing through the parenchyma from side to side.

As has been pointed out, the proglottids just behind the neck are immature and have at first no reproductive organs. These soon start to develop, the male organs appearing first, followed shcrtly after by the female structures. They are all found fully developed in each mature proglottid, which is therefore hermaphrodite.

The male gonads, the testes, consist of a number of globular follicles scattered generally throughout the parenchyma, save in the middle of the posterior end of the proglottid. They all give off delicate tubes, the vasa efferentia, which unite to form larger and larger trunks all ultimately leading to one tube, the vas deferens, about the middle of the segment. This passes transversely to one side or the other, and opens with the female aperture into a small common cavity, the **genital sinus,** on the lateral margin of the proglottid. The sinus opens by an elongated slit, the **genital pore.** The end of the vas deferens is contained in a muscular sac, and is modified to form a protrusible organ sometimes called the penis, but better termed the **cirrus.**

The female gonads, the ovaries, are two conspicuous plate-like structures lying near the posterior end of the proglottid, and joined by a transversely running canal. From the middle of this comes off the oviduct, which runs backwards towards the end of the segment, receiving shortly after its origin, the vagina. Near the posterior border the oviduct turns sharply round, receives a duct from the

yolk gland, is surrounded by the shell gland, and then passes forwards as a large median closed sac, the **uterus.** The yolk or **vitelline gland** is a conspicuous structure, composed of two lobes lying across the posterior end of the proglottid and opening into the oviduct by a single median canal. The **shell gland,** situated around and covering the bend of the oviduct, is a more diffuse gland without any special duct. The external female aperture leads into a fairly wide straight tube, the **vagina,** which passes obliquely inwards, and, as just noted, opens into the oviduct a short distance from its commencement. The inner end of the vagina is swollen out to form an oval **seminal vesicle.**

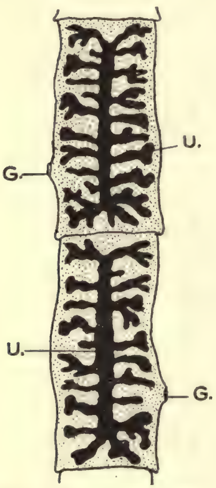


FIG. 63.—Ripe proglottid of *Tænia solium.*

G., genital aperture ; U., uterus full of eggs.

Copulation has not been observed in *T. solium,* so that it is not known for certain whether the proglottid is self-fertilising or is fertilised by another proglottid. In view of the fact that in certain allied species only one mature proglottid is present at a time, it seems probable that the former is the case. The sperms pass down the vagina and are stored in the seminal vesicle. The ova shed from the ovaries pass along the oviduct and are fertilised as they pass the entrance of the vagina. As they proceed further they become surrounded by a layer of food-laden cells from the vitelline gland, and then around each ovum and its attendant cells is secreted a thick chitinous shell, the product of the shell gland. These ova then pass on to the uterus, where they are stored and where they undergo a certain amount of development. The production of more and more eggs leads to the degeneration of the gonads and the filling up of the uterus. This is at first a simple sac, but as it fills it sends out lateral branches until it comes to occupy practically the whole of the proglottid, which is now termed ripe and is ready to be passed to the exterior with the fæces of the host. The form assumed by the branched uterus in the ripe proglottid is quite characteristic, and is often a valuable guide to the species of tapeworm. Sometimes when passed out in this way the proglottid is capable of moving about for a short time and may be swallowed whole, or more frequently it disintegrates, releasing the ova. The intermediate host in the case of *T. solium* is the pig.

While still contained in the uterus in the proglottid the egg undergoes its segmentation and grows into a tiny spherical body covered with a cuticle and provided with six chitinous hooks, and

hence known as the **onchosphere** or **hexacanth embryo.** No further development can be undergone until it is swallowed by the pig, whose digestive fluids dissolve off both the egg shell and the cuticle, releasing the tiny six-hooked embryo. This then bores its way through the wall of the gut largely by the aid of its hooks and penetrates a small blood vessel. In the blood stream it is carried about until it reaches its destination, which in *T. solium* is usually the voluntary muscles. It increases in size fairly rapidly, losing its hooks and becoming inflated with a fluid substance until it forms a thin-walled hollow vesicle about 5 mm. in diameter, known as the **proscolex.** At first this is uniform all round its periphery, but soon it thickens at one

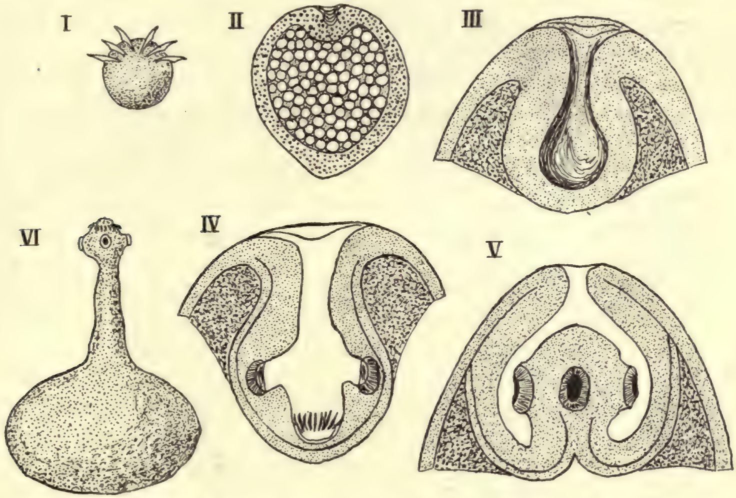


FIG. 64.—Diagram of the development of *Tænia,* adapted from Leuckart.

I., hexacanth embryo ; II., early proscolex ; III., IV., and V., anterior end of proscolex in different stages of development, more highly magnified ; V., beginning of evagination ; VI., complete evaginated scolex with caudal vesicle.

point. The thickening invaginates and is the primordium of the head of the future worm. At its inner end the invagination dilates to form a hollow vesicle, within which are produced the suckers, rostellum and spines, in fact a miniature head only inside out. By this time it has increased considerably in size, being oval and about 12 by 8 mm. in diameter, and it is known as the bladder worm or **Cysticercus.** It consists of a large vesicle, the proscolex or **caudal vesicle,** as it may now be termed, filled with fluid, and projecting into this is the introverted scolex. This marks the limit of its development in the pig, and it now remains in a passive condition embedded in the muscular tissue which secretes around it a secondary cyst of

dense fibrous connective tissue. The particular cysticercus of *T. solium* is called *C. cellulosæ,* and a piece of infected or crysticercoid pork presents a very characteristic appearance, on account of which it is commonly spoken of as " measly pork."

If pork in this condition is eaten by a human being in a raw or partially cooked condition, for thorough cooking will kill the parasite, the cysticercus becomes set free in the stomach. It evaginates its scolex and throws off its caudal vesicle, and on passing into the intestine attaches itself by means of its head to the mucous membrane. Here the posterior end of the neck starts to grow and segment, giving rise to the long tapeworm with which we started and which is ready to begin the cycle over again. It is obvious from a consideration of its life cycle that improved sanitation and the satisfactory inspection and cooking of pork can keep the parasite down; indeed in this country it has been practically eliminated, although it is still found in central Europe and may be occasionally introduced here.

Before passing on to discuss certain general problems connected with the tapeworm, it seems as well briefly to call attention to one or two allied forms that may be encountered and are of interest.

Tænia saginata.—A form that is also found in man and is on the whole very similar to *T. solium,* reaching a length of as much as thirty-six metres. It is easily distinguished from that animal by the absence of rostellum and hooks, which are replaced by an additional sucker-like structure, and also by the shape of the ripe uterus.

T. serrata.—This species has been rarely if ever found in man, but is the common tapeworm of the dog. Its cysticercus stage (*C. pisiformis*), however, is commonly met with in the mesentery of the rabbit and hare, and so encountered in dissecting the former in the laboratory.

T. echinococcus is a form consisting of but three proglottids at a time, one immature, one mature, and one ripe, and it has a very long rostellum. It makes up for its small size, about 5 mm., by being present in large numbers. It is not found in man save in the cysticercus stage, when man seems to act as an accidental secondary host. The cysticercus, known as *C. veterinorum,* or in man as *C. hominis,* produces the condition, sometimes a terrible one, known as Hydatids. The usual place for it is to be found in the liver, where it may reach the size of a child's head, and the one original proscolex gives rise by internal budding to thousands of tiny little scolices.

Dibothriocephalus latus.—As a parasite of man this " broad tapeworm," growing to a length of nine metres, is more or less confined

to Eastern countries, where it is common. The head is oval, and possesses only two lateral deep groove-like suckers. It has two external openings on the proglottid, one the ordinary genital pore, and the other that of the much curved uterus. The cysticercus is passed in the muscles of some fresh-water fish.

Dipylidium caninum is a small form, 35 c.m. in length, only rarely found in human beings, but is interesting because the genital organs are duplicated in each proglottid, each set opening by a

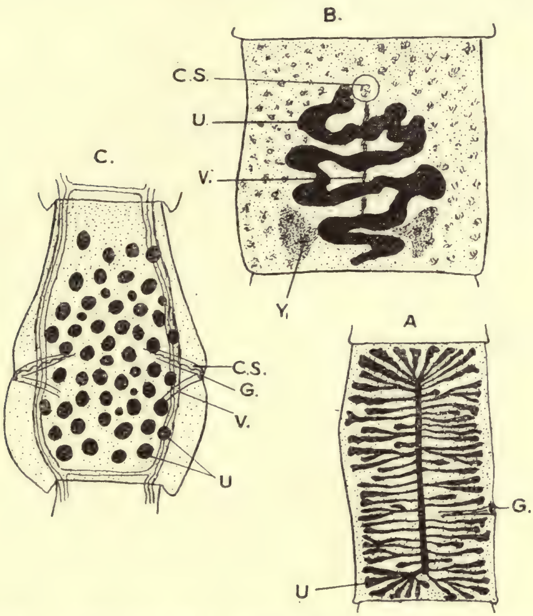


FIG. 65.—Proglottids of A, *Tænia saginata*, ripe; B, *Dibothriocephalus latus*, nearly ripe; and C, *Dipylidium caninum*, ripe.

C.S., cirrus sac; G., genital aperture; U., uterus full of eggs; V., vagina; Vi., vitellarium.

separate pore on the opposite lateral margins. Its intermediate host is a parasitic louse or flea.

Two problems call for attention in the tapeworm, its segmentation and the question of the alternation of generations.

It is obvious that there is a considerable difference between the proglottids and the somites of such a form as *Lumbricus*. In the first place new segments in the Earthworm are produced throughout the period of growth, immediately in front of the last or anal somite,

whereas in *Tœnia* they are formed at the anterior end of the chains of proglottids by the unsegmented neck—a very fundamental difference. Then, again, the only parts that are repeated in the latter animal are the reproductive organs, whereas in the earthworm the metamerism is impressed on all the various parts of the body. Lastly, as we have seen, the segmentation of the adult *Lumbricus* is founded upon a very early developed and primitive division of the mesoderm into mesodermal somites, a process not paralleled in *Tœnia*. For these reasons, among others, we cannot regard the segmented condition in the two animals as homologous or essentially similar, but as only superficially alike. How then did this condition arise in the tape-worms? The most generally accepted explanation is briefly as follows: We find the most simple and primitive members of the group are unsegmented, and have but a single set of reproductive organs situated towards the hinder end. Such an animal living in the gut might conceivably have had its posterior end broken off by the passage of the food and the peristalsis of the intestine and then proceeded to regrow the lost parts, as these lowly animals can readily do. This would be distinctly advantageous to the species, for it would bring about a greatly increased power of reproduction. The possibility of regeneration we now imagine became moved forwards in the life history of the individual, and the worm, as it were, produced several posterior ends in anticipation of their being broken off, and these had a line of demarcation between them, so that when the break did come it would not be so injurious. If this were done to a slight extent we should have a form like *T. echinococcus* with its three proglottids, or, if carried further, many proglottids, as in *T. solium*. This gives a possible mode of origin of the tape-worm condition, and so, if true, segmentation in these animals may be regarded as a special adaptation to the peculiar parasitic mode of life, and not an essential of their plan of organisation, as it is in the Annelids.

In the case of *T. solium* the egg produces a single proscolex in the muscles of the pig, and this in its turn grows directly into one adult animal, so that in this case there is obviously only a single generation with a sexual reproduction in the adult condition. *T. echinococcus* and certain other forms, on the contrary, have not such a simple life history. Their eggs produce proscolices, as in *T. solium*, but each of these in its young or cysticercoid stage gives rise by a kind of asexual budding to a large number, it may be thousands, of scolices. In these species then we have a true alternation of generations between the asexual proscolex and the sexual tapeworm. It is an additional way of securing a continuance of the species.

Finally, the tapeworms, like the sporozoa, exhibit many characteristics which are typical of internal parasites in general. With the abandonment of a free and exposed life they have given up organs of locomotion and protection against foes and evolved a means of maintaining themselves securely in their sheltered position. Their food is supplied in a readily assimilable condition that does not require an alimentary canal or its equivalent, and consqeuently we find that this and its related structures have disappeared. These two points naturally carry with them a corresponding degeneration of the nervous system and absence of sense organs. Although a convenient mode of life, so far as food supply and protection are concerned, internal parasitism implies a difficulty of re-infecting new hosts. The loss of locomotor powers makes the dissemination of the species largely a matter of chance, and as a result a vast number of eggs (or spores in the protozoa) are produced, in order to ensure that some of them at any rate shall reach another host. As a further help in spreading infection we frequently find they adopt the plan of making use of a second or intermediate host, related in some intimate way to the primary host, and this has led in many cases to the development of a complicated life history.

With *Tœnia* we close our study of the invertebrate Cœlomates, and pass on to consider the much more highly specialised Chordates.

CHAPTER VIII

VERTEBRATE ANIMALS—*SCYLLIUM CANICULA*

Introduction to Craniata—External features, *Scyllium*—Integument—Muscular system—Endoskeleton.

A Fish—*Scyllium canicula,* the Dogfish.

The next type to be studied is that of a fish, and the species taken is that known as the lesser spotted dogfish, and to the Zoologist as *Scyllium canicula.* It is practically a little shark, and is the smaller of two dogfish caught commonly around the British coasts. The larger, more rare *S. catulus*, the greater spotted dogfish or rough hound, is very similar, so much so indeed that young specimens of it are sometimes mixed in with the smaller species supplied to the laboratory, and the differences between them are so slight as to be negligible for our present purposes.

Compared with the earthworm the dogfish represents a great advance in the animal series, for it is a vertebrate animal belonging to the phylum **Chordata,** the same phylum as the frog, with which we commenced our studies, and so possessing many features in common with that animal. The **Chordata** are often divided into two groups: the Acrania, comprising a number of less familiar forms such as the lancelet *Amphioxus* and sea squirt *Ascidia*, etc., whose relation to the other members of the phylum are not clear, and all the remaining forms, the **Craniata,** marked off by the possession of a head and a vertebral column. These are the **Vertebrata** in the strict meaning of the term, and contain the following classes: Pisces, the Fish; Amphibia, the Frogs, Newts, etc.; Reptilia, the Reptiles; Aves, the Birds; and Mammalia, the Mammals. The dogfish is important because it is a representative of the Elasmobranch Fishes, one of the lowest groups, including sharks and rays, whose skeleton remains cartilaginous throughout life. This group, although specialised in some respects, retains a number of primitive features, and is consequently of considerable interest to the comparative anatomist. The primitive nature of the group is further demonstrated by the fact that the earliest known remains of fossil vertebrates belong to it.

The lesser spotted dogfish is found in shoals round the coast. It is a voracious feeder, living on other fish, on cuttlefish, octopus, crustaceans, etc., and being powerful and swift does considerable damage to ordinary edible fish. It is marketed as food, but is much coarser eating than the other, bony fish, and is consequently not widely used. Before considering it in detail it will be well to glance at some of the main characteristics of a Vertebrate which are common to the dogfish, frog and rabbit, in the types we have to study, and also, of course, to ourselves.

Like the earthworm, all the Craniates are cœlomate metazoa, and are primitively segmented, and, although this metamerism becomes partially obscured in the adult, traces of it are always to be found. The body is generally to be marked off into, at any rate, a head, a trunk and a tail. They usually lay eggs, *i.e.* are **Oviparous,** even though these may be hatched inside the mother as in some Reptiles, and an ally of the dogfish *Acanthias*, a condition termed **Ovo-viviparous.** In the higher groups of the mammals we meet with a truly **Viviparous** condition in which the young are intimately attached to the mother at a very early stage, and are brought forth alive in a fairly advanced stage of development.

The first and, perhaps, most important feature, however, concerns the skeleton which, in the embryo, is furnished by a very characteristic structure, the **Notochord** or **Chorda dorsalis.** This consists of an elastic rod of very highly modified entodermal cells that typically come from the dorsal side of the gut, and it is the presence of this same striking tissue in the ACRANIA that leads to their being grouped with the CRANIATA in the one great phylum CHORDATA. In most craniates the notochord is replaced * almost or completely by the Vertebral Column, a mesodermal structure which comes to form the main supporting axis of the body. As we have seen in the frog, this consists of a number of separate pieces or vertebræ movably articulated one with another. Not only is it a support for the animal as a whole, but it also bears on its dorsal side a canal, the Vertebral Canal, for the protection of the spinal cord. Its anterior end is modified to form a skull with which are associated upper and lower jaws.* Also more or less closely connected with the vertebral column are two pairs of limbs,* which in the fish form the fins, and in higher vertebrates the legs, though the anterior pair are sometimes specially modified to form arms or organs of flight, termed wings.

The second fundamental characteristic of a Vertebrate is its central nervous system, which is tubular in form and situated

* A somewhat aberrant group of Vertebrates, the Cyclostomes (Lampreys and Hagfish), are not taken into account.

dorsally to the notochord. This marks them off most clearly from the Invertebrates, where the nerve cord is always solid, often double, as in *Lumbricus*, and is almost invariably situated ventrally to the alimentary canal, except its most anterior pair of ganglia, which may be dorsal. The lumen of the tube in the region of the spinal cord, *i.e.* the **canalis centralis,** is quite small, but in the head region where the nervous matter enlarges to form a brain the canal also widens considerably and forms a series of hollow cavities, the ventricles, as we have observed in the frog. The central nervous system makes its appearance in the embryo as a thickened band of ectoderm in the mid-dorsal line known as the **medullary plate,** and this runs from the front to the hinder end. The edges of this plate rise up into **medullary folds,** leaving a sort of gutter, the **medullary groove,** between them. Gradually the edges come closer together until they finally meet in the middle, thus giving rise to a tubular structure, the anterior end of which even at this early stage already shows three vesicular enlargements, the rudiments of the three main divisions of the adult brain. The general ectoderm closes over the top, allowing the central nervous system to sink down. Thus from the very beginning the nervous system is a tubular structure composed of ectoderm.

The third great distinguishing point in the anatomy of the Chordata is the possession in the embryo, and sometimes, as in *Scyllium*, throughout life of a series of paired perforations in the walls of the pharynx which lead directly to the outside of the animal. These openings, the **gill slits** or **pharyngeal clefts,** are not more than seven in number, and may be just narrow clefts all the way, or enlarge to form pouches with slit-like openings to the exterior and to the pharynx. The larger part of the branchial cleft is lined with entoderm, but the ectoderm turns in over the outer portion. The slits are supported by more or less complex arrangements of cartilaginous rods termed the gill bars, the whole constituting the branchial basket. The gill slits are present throughout life in the fish and are functional in connection with the respiratory exchanges, their walls being thrown into a series of highly vascular folds, the gills. The blood, which is supplied to the gills and removed by a characteristic series of vessels, is oxygenated from, and gives up its carbonic acid gas to, the surrounding water as it passes through the capillaries of these gills.

In the classes above the fish the internal gills lose their respiratory function, which is taken on by another set of externally developed gills in some of the Amphibia, and in the rest of the Amphibia, the Reptiles, Birds and Mammals, by entirely new structures, the lungs. In spite of this, however, the clefts, or at any rate some of them,

are always developed in the embryo, together with their characteristic skeleton and vascular supply. The slits disappear entirely in the adult, with the exception of the one pair which takes part in the formation of the ear passages. Their skeleton is modified to form the hyoid apparatus, and the remains of their blood-vessels constitute the bases of the three great arterial arches of the adult.

We have dealt with the three main anatomical features of the Chordata, *i.e.* the presence of a notochord, a dorsal hollow central nervous system, and the possession of gill slits, characters which are in themselves diagnostic of the group, but the members of the group also possess a number of other points in common.

Three pairs of sense organs are present, namely, the olfactory, the optic and the auditory, which are lodged in protecting capsules more or less closely connected with the skull. The essential parts of these are always derived directly or indirectly from the ectoderm, *e.g.* the retina of the eye is developed as an outgrowth of the brain which is itself ectodermal. In the lower classes, *i.e.* Fish and Amphibia, ten pairs of cranial nerves come off from the brain with the same origin and similar general distribution, being obviously homologous. The higher classes, *i.e.* Reptiles, Birds and Mammals, have in addition to these nerves two more cranial nerves, making twelve altogether.

The alimentary canal is a long folded tube running from an anterior ventral mouth to an anus that is posterior and ventral, and it is differentiated into distinct regions. The portion of the gut just beyond the stomach receives the ducts of a well-marked liver and pancreas. The liver has not only an arterial blood supply, but a special series of veins forming the **hepatic portal system** gathers up the blood from the intestine and conveys it to the liver.

The vascular system is composed of a closed series of vessels carrying the blood to and from the central organ, the heart, which is composed of chambers separated from one another by valves. The blood is composed of an almost colourless fluid, the **plasma,** in which float large numbers of corpuscles, some white, and others, far more numerous, red, owing to the contained hæmoglobin.

The kidneys are compact bodies composed of a number of urinary tubules aggregated together and possessing a common duct, the ureter, for the conveyance of the urine to the exterior. In addition to the glands connected with the gut and skin possessing ducts for the removal of their secretion, there are also a number of ductless glands whose products are passed directly into the blood stream.

The skin is composed of an outer epidermis of ectodermal origin and an underlying dermis derived from the mesoderm, and except

in a number of living Amphibia it bears exoskeletal structures in the form of scales, feathers or hairs.

External Features and Integument.

FIG. 66.—The rough hound—from Borrodaile.

Note mouth, eye, spiracle, lateral line, gill clefts, pectoral and pelvic fins, dorsal fins, caudal fin, vertical fins between caudal and pelvic fins.
cf., upper lobe of caudal fin : *cf*[1]., lower lobe of the same ; *pl.f.*, pelvic fin.

The dogfish is bilaterally symmetrical with a greatly elongated spindle-shaped body admirably adapted for swimming, and it may reach a length of about two feet. *S. catulus* is much larger, and may grow to almost double this size. The body is divisible into three regions : the head extends back to the beginning of the pectoral fin and contains the skull, sense organs, buccal cavity and pharynx ; the trunk stretches from that point to the cloaca, and contains the main circulatory organs, the viscera and the cœlom which is confined to this region ; lastly, the remaining part, which occupies slightly more than half the total length, is the tail forming a very efficient organ of progression.

The fins form a very striking series of thin flat expansions supported by skeletal elements, and are divisible into two groups, the median or unpaired fins, and the lateral or paired fins. Of the four median fins two are placed in the mid-dorsal line, the foremost and larger, or **anterior dorsal** fin, is about half-way back, and the posterior dorsal fin about two-thirds of the way back. They are triangular in shape, and the anterior of them in the sharks projects from the water when the animal is basking just beneath the surface, and so constitutes for sailors in warmer seas a significant indication of the presence of these voracious fish. The **ventral fin** is a similar but blunter fin in the mid-ventral line situated at a distance intermediate between the two dorsal fins from the front of the animal. The fourth of the unpaired fins, and by far the largest, is the **caudal fin**. It commences about three-quarters of the way back as a low ridge, and increasing in height passes right round the posterior end of the tail on to the ventral surface. It will be seen on closer inspection

that the tip of the vertebral column turns up at an angle. The caudal fin round this and on the ventral side is expanded into a bifid lobe larger than the dorsal lobe, and with its anterior part larger than the posterior. The result is a markedly asymmetrical structure, and it constitutes what is termed a **Heterocercal tail.** This is a highly specialised form of fin derived from a much more primitive type, the **Diphycercal fin,** such as we find in the tadpole and young dogfish. In these the vertebral column remains straight, and the fin is evenly balanced around it, terminating in a point. In the common bony fish a balanced condition is also to be found, but it is secondarily acquired. The tip of the vertebral column is turned up as in *Scyllium*, but the simple ventral lobe is prolonged backwards, producing the characteristic "fish tail." This condition is designated **Homocercal.** There seems little doubt that the median fins are to be regarded as phylogenetically older than the paired fins. Not only do they develop earlier, *i.e.* are ontogenetically older, but there are forms like *Amphioxus* and fishes like the Lampreys and Hagfish in which they alone are present and no sign of paired fins are to be found.

The larger of the paired fins are the pectoral fins, triangular structures arising by their apices from just behind the gills, ventrolaterally about a quarter of the way back. The pelvic fins are smaller, lying in the ventral part of the body and arising not quite half-way back just in front of the cloaca. They differ in the two sexes, and so for the first time in the higher animals we find an external character that enables us readily to distinguish the two sexes. In the female the mesial borders of the pelvic fins pass backwards behind the cloaca parallel with one another and quite free. In the male, however, these two borders unite to form a sort of elongated pouch within which is situated on each side of the middle line a rod-shaped body, the **Clasper.** These claspers or copulatory organs are grooved on their inner surface and bear at their extremity a group of papillæ, on which the scales point in the reverse direction. They are used during copulation, and serve for the conveyance of the sperms to the oviducts. The paired fins are of great interest, as they are homologous with the fore and hind limbs of higher Craniates, and so with our own arms and legs. Their actual mode of origin is not quite clear, but the most generally accepted account is that they are modified local remnants of a continuous lateral fold running forward from the cloaca to the branchial region; but we shall return to this point later.

The fins, median and paired, are all concerned with locomotion in water. The propellant power is obtained from vigorous strokes of the powerful tail with its strong fin, steering is mainly carried out

by the pectoral fins, and the dorsal, ventral and pelvic fins act as steadying or equilibrating organs.

The head is somewhat flattened, and of a triangular shape, ending in a bluntly rounded snout. On the sides of the head are situated the eyes. They are provided with upper and lower lids, the latter are able to be pulled right up over the eye. The external nares are two approximately circular openings on the ventral surface of the head, a short distance from the front of the snout. Each leads into a hollow cavity, the nasal sac or olfactory organ, which has no internal narial passage such as we find in the frog. On the other hand, the nasal sac communicates with the mouth by means of a deep groove, the naso-buccal or oro-nasal groove, which is partly covered by a flap-like extension of the skin termed the fronto-nasal process. This is a very primitive condition, and one that is met with in the embryos of the higher Craniates. It is a failure in the complete transformation of this into an internal nasal passage in man that leads to the condition known as cleft-palate or hare-lip. Just behind the olfactory organs is the large mouth of a crescentic shape, and provided with a formidable armament of many rows of strong pointed teeth. A short distance behind the eye is a small circular orifice, the **Spiracle,** which leads into the pharynx. In spite of their anterior position and appearance these perforations are homologous with true gill clefts, and their development shows that they are in reality the foremost of the series. Indication of the fact that they were at one time similar to the other clefts is to be found in the presence of a tuft of rudimentary gill filaments, the **pseudobranch,** situated on their anterior wall. They appear to be mainly concerned with the intake of water for respiratory purposes. It is the spiracular cleft, lying as it does in close proximity to the auditory capsule, that takes part in the formation of the ear passages of higher vertebrates.

A short distance further back on each side are a series of five vertical slits decreasing in size from the front, these are the external gill clefts. When they are opened it will be seen that they lead into a corresponding series of branchial pouches. The anterior and posterior wall of each pouch, save the hinder wall of the last, is thrown into a series of radiating folds, the **branchial filaments** or **gills,** which are delicate and very vascular, so that they appear bright red in life or in a freshly killed fish.

There remain for mention two apertures on the dorsal surface of the head, so small as to be practically invisible, although their position may be demonstrated in a fresh specimen by pressing the back of the head which causes drops of a milky fluid to be exuded. They lie in the mid-dorsal line just about on a level with the front of

the spiracles, and are the openings of the endolymphatic ducts leading down to the membranous labyrinth of the ear.

Scattered over the head, particularly in the snout region, are a number of small apertures leading down into tiny tubes, the **mucous canals,** which are filled with a gelatinous substance that is extruded if the head is squeezed. A similar series of apertures leads into a regular series of canals above and below the orbits, and on the dorsal and ventral sides of the hinder end of the head. These are connected near the spiracle with a pair of canals that run along the whole length of the fish, one on each side, in a shallow groove of lighter colour, and so are easily discernible ; they constitute the so-called **lateral line canals** and lodge a series of sense organs.

As we have already noted, the **vent** or **cloaca** is situated between the hinder internal margins of the pelvic fins. It is a short slit leading into a shallow cloacal chamber into which open the hinder end of the alimentary canal, the urinary and genital apertures. The anus proper or termination of the gut opens into the front end of the cloacal chamber. Further back are two small cavities, the cloacal pits, partly overhung by a flap of skin, the cloacal papilla. Anteriorly the pit ends blindly, but it is continued back as a minute canal, the **abdominal pore,** leading into the cœlom, which thus communicates directly with the exterior, a condition not found in the higher craniates. A considerable amount of variation is met with in this pore showing that it is of small functional importance, and probably represents a vestigeal structure. Sometimes it is present on one side only, sometimes on both sides, or again it may be absent altogether. The two sexes have their urinary and genital apertures differently arranged. In the male there is a small projection, **the urinogenital papilla,** perforated by a single pore. It lies in the middle line just behind the anus and in front of the cloacal pits, and serves for the transmission of excretory and reproductive products. The female possesses a structure similar in appearance, but serving only for the passage of the urine and so constituting a **urinary papilla.** The **oviducal opening** in the female is a fairly large longitudinal cleft on the dorsal wall of the cloacal chamber between the papilla and anus. It leads directly to the two oviducts, which run together just at this point.

Skin and Exoskeleton.

The skin of *Scyllium,* like that of *Rana,* is composed of two layers, an outer, the epidermis, derived from the ectoderm, and an inner layer, the dermis, of mesodermal origin. The epidermis is a stratified epithelium with a layer of cubical actively dividing cells, the Malpighian layer, at the base. As they pass outwards the

cells become more and more flattened. Scattered among them here and there are spherical glandular or **mucous cells,** which are not aggregated to form glands as in the frog. The dermis is composed of two layers, an outer of connective tissue, and a lower thicker layer of tough fibrous tissue. It contains blood-vessels and nerves and a number of pigment cells arranged in groups to form the well-marked spots. The skin is rough to the touch, particularly if the hand be drawn from behind forwards, owing to the presence in it of small close-set scales with projecting points directed backwards and

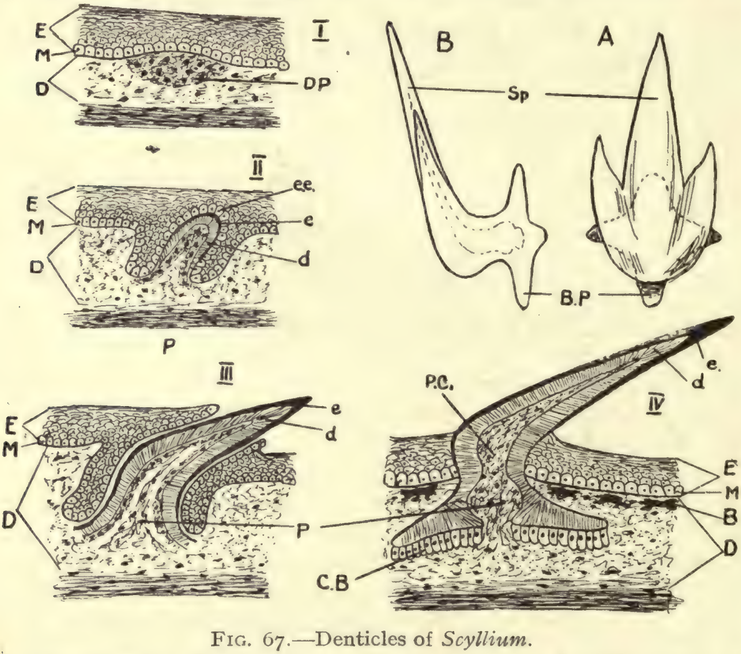


FIG. 67.—Denticles of *Scyllium*.

A., surface view of denticle; B., side view of denticle: I.–IV., successive stages in the development of a denticle.
C.B., formative cells of basal plate; D., dermis; *d.*, dentine; D.P., dermal papilla; E., epidermis; *e.*, enamel; *e.e.*, enamel epithelium; M., Malpighian layer; P., pulp; P.C., pulp cavity; Pi., pigment cell.

forming a characteristic exoskeleton. When dried the skin is known commercially as **shagreen**, and is utilised for polishing purposes. These scales are of a peculiar type known as **placoid scales** or **dermal denticles,** and in their production both epidermis and dermis take part. They differ completely from the scales of the ordinary bony fish, which are entirely dermal structures.

A denticle consists of a quadrangular basal plate and a blade or spine set at an acute angle to this. The **basal plate** lies firmly

embedded in the upper part of the dermis, while the spine, which is generally leaf-shaped with a long point flanked on each side by a shorter one, projects through the epidermis. The greater part of the scale consists of hard calcareous substance, **dentine,** a dermal product, covered with a layer of still harder **enamel** secreted by the epidermis. The denticle is hollow, containing within it a pulp cavity in the form of a median canal with side branches which opens to the outside by means of a more or less circular hole in the basal plate. In life this cavity is filled with a loose connective tissue, the pulp, containing blood-vessels, lymph-vessels, and nerves which pass in through the hole in the base. The pulp is surrounded by a single layer of characteristic cells known as **odontoblasts,** the function of which is to secrete the **dentine.** This dentine, unlike bone, contains no cells within it, and therefore grows only on the side next to the odontoblasts. Its matrix contains a very high percentage of calcium salts, considerably more than in bone, and is penetrated by a number of extremely fine processes from the odontoblasts which lie in tiny branched **dentinal tubules.** The enamel or **vitrodentine,** as it is termed, has a still higher proportion of calcium salts, and is in consequence harder. Although it does not possess the prismatic structure characteristic of the enamel of our own teeth, it is probably homologous with it.

It will be remembered that the lining of the buccal cavity is essentially the same as the skin covering the body, and, although most of it is devoid of exoskeletal structures, as it passes over the jaws it produces a series of rows of highly modified denticles, the teeth. These have the same fundamental structure as the ordinary scales, which owe their name of denticles to this similarity, and from which they have undoubtedly been derived. The blade, however, is broader and not so long, and the median spine has two or three spines on each side of it, all being of approximately the same length. The enamel layer is also considerably thicker. Various modifications of the denticles produce the characteristic spines and teeth met with in all the Elasmobranchs.

The development of a denticle calls for notice owing to its similarity with that of our own teeth. The first indication of the formation of a scale is the aggregation of a number of the cells of the superficial layer of the dermis to constitute a **dermal papilla,** and this represents the origin of the pulp. This papilla enlarges and presses upwards into the epidermis, the Malpighian layer of which becomes modified to form a layer of columnar cells, the **enamel epithelium.** While this is taking place, the outermost cells of the papilla become transformed into odontoblasts which secrete the dentine, first in the form of a small cone capping the papilla. The base of the papilla

narrows off considerably, but always remains open, and the whole structure sinks down into the dermis, below the level of the epidermis, causing the enamel epithelium and the adjacent cells of the Malpighian layer to become infolded in a very characterictic manner. The main part of the papilla remains to form the pulp, which with the odontoblasts and dentine of the blade and entire basal plate, by far the largest part of the denticle, is the product of the dermis. The enamel alone, at any rate the greater part of it, comes from the epidermis, and, according to some authorities, this also receives contributions from the underlying dentine.

The second variety of exoskeletal element in the dogfish takes the form of fairly long cartilaginous rods or rays supporting the distal parts of all the fins. In consequence of their being developed in the dermis they are termed dermal fin rays or **dermotrichia.**

Muscular System.

The muscles of the dogfish, like those of the frog, are of two varieties, striate and non-striate. The latter, including also the

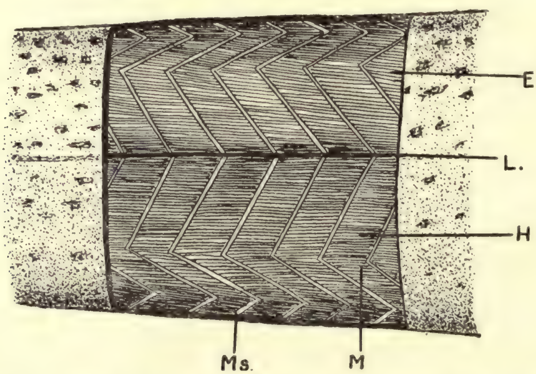


FIG. 68.—Sketch to show arrangement of myotomes in *Scyllium*.

E., epiaxial myotomes ; H., hypaxial myotomes ; L., lateral line ; M., myotome ; Ms., myosepta.

cardiac muscles, are confined to the various viscera. If the skin be stripped off the body muscles will be seen beneath it arranged in a very characteristic manner. Unlike the frog, the fibres are not bound together to form definite discrete muscles, save in certain parts, but arranged in narrow columnar sheets. These extend from the lateral line dorsalwards and ventralwards in parallel zigzag strips known as **muscle segments** or **myotomes,** which meet in the mid-dorsal and mid-ventral line and alternate with the vertebræ, a

very primitive arrangement indicating clearly a metameric segmentation. They are separated by thin fibrous sheets of connective tissue, the **myosepta** or **myocomata,** to which the individual fibres lying in the longitudinal direction are attached at each end. The lateral line, which is partly embedded in a thick horizontal myoseptum, separates the muscle segments into a dorsal or **epiaxial** series of broader and a ventral or **hypaxial** series of narrower myotomes. In the region of the eye, of the jaws and of the fins the fibres are bound in bundles to form discrete muscles more like those of *Rana.*

Endoskeleton.

As in the frog, the endoskeleton may be divided for description into axial and appendicular portions. The axial part is composed of the vertebral column and the skull, which in its turn is formed by the cranium and a somewhat complex visceral skeleton. The appendicular skeleton consists of the median fin supports, and the pectoral and pelvic girdles with their corresponding limbs. The endoskeleton as a whole is remarkable in that it always, even in the adult, remains in a cartilaginous condition, no true bone ever being developed although it is much strengthened by calcification, *i.e.* the deposition in it of calcium salts in certain parts of the vertebral centra.

The vertebral column is a very primitive one, and composed of a long series of vertebræ whose constituent parts are not nearly so completely fused as in *Rana,* and so can be recognised as separate pieces. It contains quite considerable remains of the notochord in the adult. The centra are short stout cylinders with a deep conical hollow at each end, a condition known as **amphicœlous,** and one, it will be remembered, that is retained in the eighth vertebra of the frog. The internal faces of the two hollows are lined with calcified cartilage and communicate with one another by a small central hole, the cavities of the hollows and the central holes being filled with the persistent notochord. The centra are firmly bound together by tough fibrous bands of tissue, the **intervertebral ligaments,** which pass externally over the notochord. Dorsally they bear two sets of cartilaginous plates which constitute the neural arches, and together with a third set form a closed vertebral canal in which lies the spinal cord. From the latero-dorsal aspect of the centrum arises a pentagonal plate, the **vertebral neural plate,** which is only about half the length of the centrum. Filling in the interstices between these are hexagonal **intervertebral neural plates,** lying above the intervertebral ligaments and so completing the neural arches. Fitted into the notches left on the dorsal edges of the plates is a third series, a row of unpaired, somewhat wedge-shaped cartilages, the neural

spines. A foramen at the lower posterior border of the vertebral neural plate and a similar one at the upper posterior border of the intervertebral neural plate lead into the vertebral canal. These allow for the passage of the ventral and dorsal roots of the spinal nerves respectively, and from their positions it is obvious that the ventral root arises in front of the corresponding dorsal root.

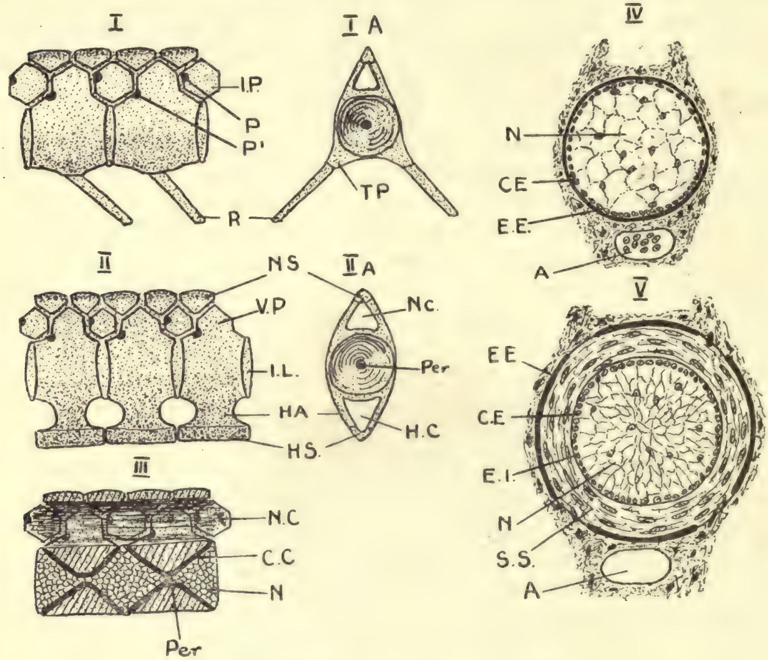


FIG. 69.—Vertebral column of *Scyllium*.

I., lateral view of two vertebræ in anterior body region; I.A., end-on view of vertebra in same region; II., lateral view of two vertebræ in tail region; II.A., end-on view of tail vertebra; III., median section of two vertebræ in body region; IV. and V., two successive stages in the early development of the centrum;—adapted from Hasse.

A., aorta; C.C., calcified cartilage; C.E., chorda epithelium; E.E., membrana elastica externa; E.I., membrana elastica interna; H.A., hæmal arch; H.C., hæmal canal; H.S., hæmal spine; I.L., intervertebral ligament; I.P., intervertebral neural plate; N., notochord; N.C., neural canal; N.S., neural spine; P.P1., apertures for the exit of the dorsal and ventral roots of a spinal nerve; Per., perforations through centre of the cartilage of the centrum; R., rib; T.P., transverse process; V.P., vertebral neural plate.

From the ventro-lateral edges of the centra in the middle region of the body two short projections, the **transverse** or **hæmal processes,** project outwards. To the end of each of these is attached a fairly long slender rod of cartilage, **the rib,** which lies laterally in the main horizontal septum between the epi- and hyp-axial myotomes, and is also in the planes where this septum is joined by the ordinary

myosepta. The hæmal processes of the anterior trunk vertebræ are reduced to mere ribless stumps, while in the caudal region they are greatly expanded and pass off more ventrally as flattened plates to curve inwards and meet in the middle line. They are completed by a series of mid-ventral **hæmal spines,** which are the bases for the support of the ventral portions of the caudal fin. In this way another tube, the **hæmal canal,** is formed beneath the centra, similar to the neural canal above them, and in life this contains the caudal artery and caudal vein, the main vessels of the tail.

Turning now to consider the development of the vertebral column, we find that the first part of the skeleton to make its appearance in the embryo is a structure known as the **notochord** or **chorda dorsalis,** which arises as a rod of cells derived from the dorsal part of the entoderm of the gut. It is, therefore, ventral to the central nervous system under which it stretches from the posterior end to just below the fore-brain, where it becomes thin and runs off into a downwardly turned end. The cells, disc-shaped to start with, soon secrete around themselves a clear refractive elastic membrane, the so-called **primary chordal sheath** or **membrana elastica externa.** The cells enlarge and become vacuolated by the formation within them of a jelly-like substance, and so exhibit in section, a characteristic appearance producing the typical notochordal tissue. The vacuoles fill the inside of the cells, and so reduce the cytoplasm to an enveloping layer. At first scattered, the nuclei migrate to the periphery of the chorda, there forming a layer termed the chorda epithelium. This soon secretes a second thicker and more fibrous layer within the former, and termed the **secondary chordal sheath** or **membrana elastica interna.** The mesoderm (mesenchyme) surrounding the chorda produces migrant cells which wander into the inner sheath and gradually transform it into a thick cellular layer, now termed the **tunica skeletogena.**

From this a large part of the centrum is formed ; the neural arches, etc., are laid down in an extension of the mesenchyme layer which encloses the notochord and passes up to surround the spinal cord, and is called the **skeletogenous sheath.** In this are differentiated four longitudinal bands of deeper staining more tightly packed cells, two dorso-lateral and two ventro-lateral. Paired cartilages appear in the bands, and on the dorsal side are the beginnings of the vertebral and intervertebral neural plates, and on the ventral side the hæmal arches. Vertical rings of cartilage are now laid down in the tunica skeletogena corresponding in position with the arches, and these constitute the primordia of the centra. As they grow they become much thicker in their central region, thus constricting the notochord intracentrally, but they always leave a

small hole in the middle. Intervertebrally the chorda is not constricted, but retains its original size, so that in median longitudinal section it appears as a series of diamonds strung together. The centrum is finally completed by the growth around it of a thin extension of the bases of the arches. Each vertebra is thus composed of a number of parts which develop separately, but all come from mesenchyme. Between the vertebræ the tunica skeletogena is transformed into the strong fibrous intervertebral ligament.

Skull.

The skull of the dogfish remains in a cartilaginous condition throughout life, and furnishes a very good example of a primitive vertebrate skull which is not modified as in the higher Craniates by the addition of bony structures developed either in the cartilages or the surrounding membranes. It consists of a **cranium** or brain case, with which are fused the olfactory and auditory capsules, and to which are connected a series of seven paired segmental visceral arches which originate as supporting elements in relation to the perforations of the pharyngeal walls known as the gill clefts.

The **chondrocranium** of *Scyllium*, so called to indicate that it remains cartilaginous throughout life, is shaped like a slightly flattened oblong box within which lies the brain. Its floor and front end are complete, and so also are the two long sides, save for a number of small perforations through which nerves or blood-vessels pass. The hinder end is wide open, leaving a large hole, the **foramen magnum,** through which the brain is continuous with the spinal cord. The cartilaginous roof is incomplete at the anterior end, where there is situated a large elongated oval opening, the **anterior cranial fontanelle,** closed, however, by a membrane.

The hinder region of the cranium is formed by a ring of cartilage surrounding the foramen magnum, and it is termed the **occipital region.** It bears ventro-laterally of the foramen two rounded smooth prominences, the **occipital condyles,** whereby the cranium articulates with the front end of the vertebral column. The cranial floor between the condyles is formed by the **basal plate** of cartilage which runs forward as far as a small median perforation, the **internal carotid foramen,** through which the similarly named artery enters the brain case. The portion of the cranium immediately in front of the occipital is known as the **otic region,** and it is greatly expanded owing to the fact that it has fused with it the large **auditory** or **otic capsules** in which are lodged the structures of the internal ear. Clearly showing on the roof of the auditory capsule are two ridges marking the position of the anterior and posterior semicircular

canals, and on its side is a similar ridge indicating the horizontal semicircular canal. The two ridges of the vertical canals on each side converge to a median oval depression in the roof of the cranium in which lie the two apertures of the **endolymphatic ducts** (**aqueducti**

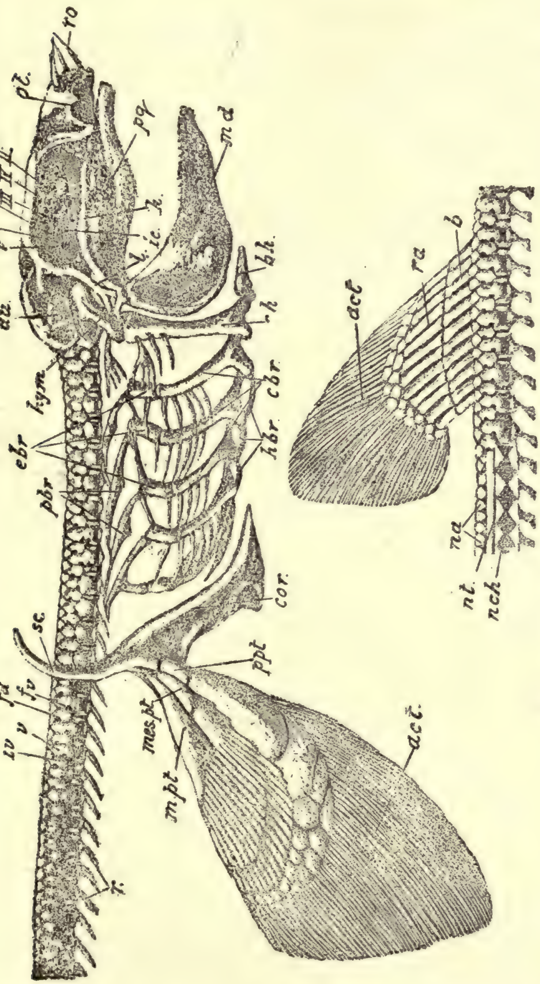


FIG. 70.—*Scyllium canicula.*—From Bourne.

The upper figure represents the skull, visceral skeleton, the anterior part of the vertebral column and the pectoral girdle and fin of *Scyllium canicula*. The lower figure shows the skeleton of the first dorsal fin attached to a section of the vertebral column; the last few vertebræ have been cut through vertically. In the skull—*au.*, auditory capsule; *ol.*, olfactory capsule; *ro.*, rostrum; *pg.*, palato-quadrate cartilage; *md.*, mandibular cartilage; *l.*, post-spiracular ligament; *II.*, optic foramen; *III.*, foramen for 3rd nerve; *IV.*, foramen for 4th nerve; *V.*, foramen for main branch of 5th, 6th, and main branch of 7th nerve; V^a., VII^a., foramina for ophthalmic divisions of the 5th and 7th nerves; *h.*, foramen for hyoidean artery; *i.c.*, interorbital canal. In the vertebral column—*v.*, vertebral plate; *i.v.*, intervertebral plate; *f.d.*, foramen for dorsal root, and *f.v.*, foramen for ventral root of a spinal nerve. In the visceral skeleton—*hym.*, hyomandibular cartilage; *bh.*, basihyal; *ch.*, ceratohyal; *pbr.*, pharyngobranchials; *ebr.*, epibranchials; *cbr.*, ceratobranchials; *hbr.*, hypobranchials; the gill-rays are shown on the epi- and ceratobranchials and on the hyomandibular and ceratohyal cartilages. The extra branchial cartilages are omitted. In the pectoral girdle—*sc.*, scapula; *cor.*, coracoid; *ppt.*, propterygium; *mespt.*, mesopterygium; *mpt.*, metapterygium; *act.*, tactinotrichia. In the lower figure—*b.*, basals; *ra.*, radials; *act.*, actinotrichia; *na.*, neural arches; *nt.*, spinal cord; *nch.*, the notochord constructed intravertebrally.

vestibuli). In front of this region, again, the side of the cranium is hollowed out slightly for the lodgment of the eyes or **optic capsules,** so that it is termed the **optic region.** The hollowing is accentuated by the roof and floor of the brain case, being carried out laterally into flat wing-like expansions known as the **supra-** and **infra-orbital**

ridges respectively. The former continues into the nasal capsule in front, and the auditory capsule behind. These capsules, together with the ridges, constitute an efficient orbit within which lies the eyeball attached to the lateral cranial wall by the optic nerve and a series of muscles.

The anterior end of the orbit is also in part formed by a **pre-orbital** or **lateral ethmoidal process** continuous with the hinder wall of the olfactory capsule. This with the remaining part of the skull in front of it, composed almost entirely of the nasal capsules, is known as the **ethmoidal region,** and into it the cranial cavity does not enter. The olfactory capsules are thin-walled hollow spherical structures, each with a large opening on the ventral side. They are completely separated from one another by an extension of the cranial floor known as the **mesethmoidal plate** or **internasal septum.** This, again, is prolonged as a slender rod, the rostral cartilage, which together with two similar cartilaginous bars arising from the antero-dorsal walls of the capsules constitutes the rostrum or skeletal support of the snout.

Let us turn now to consider the perforations in the side walls of the cranium. At the antero-ventral corner of the orbit, which is occupied by a large blood sinus, is the **orbito-nasal foramen,** placing the orbital sinus in communication with the nasal sinus. Midway along the orbit in its lower portion is the conspicuous **optic foramen,** through which the optic nerve passes. In the postero-ventral corner is another large perforation for the exit of the main branches of the fifth and seventh and the entire sixth cranial nerves. Between this and the optic foramen are three smaller holes for blood-vessels. The most anterior of these is for the hyoidean artery, the posterior for the internal carotid artery, and the middle one, slightly more dorsal than the others, is the **interorbital canal,** which puts the two orbital sinuses in communication. The remaining foramina in the orbit are nearer the dorsal side of the cranium. In the postero-dorsal corner is a foramen for the ophthalmic branch of the seventh cranial nerve which runs forward in a shallow groove. Just below, and in front of this, is a similar aperture for the ophthalmic branch of the fifth cranial nerve, from which also a groove passes forward soon uniting with the former. Running forward to the front end of the orbit, the common groove passes out on to the dorsal side of the supra-orbital ridge by a well-marked hole. Antero-ventrally of the foramen for the fifth ophthalmic nerve lies that of the third cranial nerve, and just dorsal to and in front of this, again, is another for the fourth nerve. From the posterior border of the orbit below the ridge of the horizontal semicircular canal runs a well-marked furrow in the wall of the optic capsule, the **post-orbital groove,** in

which is a vessel joining the orbital to the anterior cardinal sinus. A short distance along this is a foramen transmitting the ninth cranial nerve, which comes from the floor of the capsule wherein it runs, and at its posterior end another perforation just lateral of the occipital condyles forms the exit for the vagus.

The development of the cranium in the dogfish is interesting, since it is similar in its early stages and main outlines to that of any typical Craniate. The first skeletal structure in all these forms is, as has already been pointed out, the notochord, which in *Scyllium* runs under the brain as far forward as the hinder end of the fore-brain, *i.e.* up to the level of the pituitary body. Two separate regions of development of the cranium are consequently to be noted, a posterior chordal region, comprising the occipital and otic regions of the adult, and an anterior pre-chordal portion later forming the orbital and ethmoidal regions. The first cartilages to appear in the hinder region are two bars, **the parachordals,** one on each side of the notochord, which subsequently fuse around this to form the basal plate. In its occipital region this shows signs of segmentation, suggesting its derivation from a modified anterior part of the vertebral column,* but there are no such indications in the otic region. To the sides of this latter lie the beginnings of the membranous labyrinth, the **auditory vesicles,** around which a cartilaginous capsule is soon developed. In the pre-chordal region also the first elements to appear are two cartilaginous bars, the **trabeculæ cranii,** and these two fuse to form a **trabecular plate.** Their hinder ends, however, remain open for a time, leaving the **pituitary fontanelle,** but later grow together below the hypophysis cerebri, which thus comes to be lodged in a depression in the cranial floor. At its front end the trabecular plate is continued on to form the internasal septum.

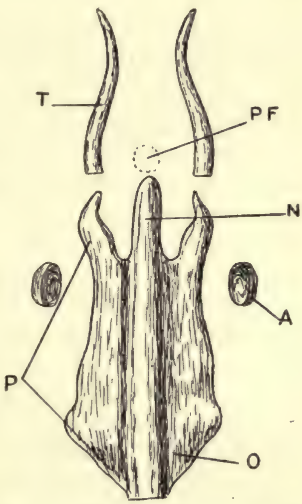


FIG. 71.—Development of cranium in a Craniate, adapted from Ziegler's model.

A., auditory capsule ; N., notochord ; O., occipital region : P., parachordal ; PF., future position of pituitary fontanelle ; T., trabecula cranii.

The side walls of the occipital region are formed by lateral

* This suggestion is also supported by other evidence into which we cannot enter here.

upgrowths of the basal plate, while in the otic regions they are composed of the mesial walls of the auditory capsules. In the orbital regions only a small part of the side wall is derived from upgrowths of the trabecular plate ; it is mainly built up from two independent dorsal elements, the **orbital cartilages.** These meet in the middle line posteriorly, forming a cranial roof, and they also fuse with the otic capsules. At the front end, however, they remain apart, leaving between them the anterior cranial fontanelle. The rest of the anterior end of the skull is formed by the cartilaginous nasal capsules which are laid down around the **olfactory vesicles.**

Visceral Skeleton.

In *Scyllium* there is also connected with the skull a visceral skeleton composed of seven pairs of arches one behind the other, each composed of two half hoops of cartilage forming a support for the anterior end of the alimentary canal. None of these are actually fused with the cranium, although the first two are firmly attached thereto by means of ligaments. The first arch is the mandibular, composed of upper and lower jaws. The upper jaw or **palato-pterygo-quadrate cartilage,** is a stout curved bar of cartilage somewhat compressed laterally and situated in the upper margin of the mouth. Its anterior end curves inwards to the middle line to meet its fellow in a ligamentous **mandibular symphysis,** and it is attached to the cranium just behind the olfactory capsule by the **ethmo-palatine ligament.** The posterior end is markedly flattened and bears a strong ridge for the attachment of powerful jaw muscles, and it further bears at its postero-ventral corner a surface for articulation with the lower jaw. The lower jaw itself is similarly composed of two flattened curved bars, **Meckel's cartilages,** lying in the lower margin of the mouth, and they also meet in an anterior median ligamentous symphysis. The cartilage is narrow in front, but much deeper behind for the insertion of muscles, and here it not only articulates with the upper jaw, but the two jaws are connected with the hyomandibular cartilage. It is noteworthy then that neither jaw is directly joined to the cranium, but only indirectly through the intermediation of ligaments and the upper portion of the second or hyoid arch. Such a skull is termed **Hyostylic,** in order to distinguish it from an **Autostylic** one such as our own, in which the jaws are directly connected with the cranium. It will be seen later that the mandibular arch is much modified from a typical arch, and both parts of it are covered by an integument bearing numerous rows of sharp close-set teeth which are homologous with dermal denticles. The folds of skin at the side of the mouth are supported by a pair of

elongated labial cartilages, of which the dorsal in the upper lip is the larger.

The second or **hyoid arch** more nearly approaches in structure a typical branchial arch, and it is divided into two portions. The dorsal end, the **hyomandibular cartilage,** is a stout short rod lying just behind the spiracle, which articulates with the auditory capsule just below the post-orbital groove. This bar is firmly connected with the jaws by the stout **symplectic ligament,** and so suspends them from the cranium, being for this reason sometimes termed the suspensorium. To its ventral end is also attached the lower portion of the arch, namely, the **ceratohyal cartilage.** This is a long curved structure more slender than the hyomandibular, and it runs antero-ventrally under the lower jaw to become attached in the middle line to a median **basihyal plate,** lying in the floor of the pharynx and buccal cavity. A thick ligament joins the ceratohyal to the lower jaw. Two other ligaments just behind the spiracle help to keep the jaws and hyoid arch in position: the first is the superior post-spiracular ligament running from just above the anterior end of the post-orbital groove to the end of the palato-quadrate and hyomandibular cartilages; the second, the inferior post-spiracular ligament, passes from the postero-lateral border of the floor of the skull below the orbit to the hyomandibular and ceratohyal. Both portions of the hyoid arch bear a series of small cartilaginous rods, the **branchial rays,** on their posterior edges which serve for the support of the front wall of the first gill cleft.

It will be seen, then, that the spiracle lies in front of the hyoid arch, and between it and the mandibular, although the latter turns forward parallel with the cranial floor, and we find the anterior spiracular wall strengthened by a small **prespiracular cartilage,** probably the remains of the branchial rays at one time carried by the mandibular arch in an ancestral form.

The remaining five visceral arches are the **branchial arches,** numbered 1 to 5 from before backwards. Each becomes split up into four distinct segments and, connected together by a median ventral unpaired **basibranchial plate,** form a series of supporting bars for the walls of the branchial pouches. The branchial clefts receive their name from the skeletal element immediately behind them, so that the spiracle is more properly termed the **hyoidean cleft,** and the rest the true branchial clefts, although, of course, they are strictly homologous. The four segments of the arch on each side are in order dorso-ventrally the **pharyngeo-, epi-, cerato-** and **hypo-branchials.** The pharyngeo-branchials are elongated triangular plates that run from just beneath the vertebral column forwards and outwards in the roof of the pharynx, and the fourth and fifth are

joined by the fusion of their dorsal extremities. The epibranchials are short stout rods lying almost vertically in the side walls of the pharynx and articulating dorsally with the pharyngeo- and ventrally with the cerato-branchials. These latter are more elongated rods passing forwards and inwards in the ventral pharyngeal wall. The hypobranchials are not so regular as the other elements. The first pair are short slender rods running forward and joining the first cerato-branchials to the basihyal. Hypobranchials 2, 3 and 4 are also small rods, but running backwards; the first pair join in the middle line and also connect with the succeeding pair, while the third and fourth pairs put their respective arches in connection with the basibranchial plate. The fifth arch lacks a hypobranchial, its ceratohyal, which directly abuts on to the basibranchial, is much expanded and has a conspicuous notch at its postero-lateral corner through which an important blood-vessel, the ductus Cuvieri, passes. The basibranchial plate is a median flattened sheet of cartilage helping to form the roof of the pericardial cavity. The posterior borders of all epi- and cerato-branchials, except the fifth, bear a series of small unbranched branchial rays. In this manner is constituted a fairly complex skeletal framework, the branchial basket. Other series of curved rod-like elements, the **extra branchials,** are developed just below the skin in relation to the second, third and fourth arches, but as they are not firmly attached to the other branchials they are often missing in prepared skeletons. The relation of the various parts of a typical visceral skeleton may be represented as follows :—

VISCERAL SKELETON.	A. First arch mandibular	Upper jaw (palato-pterygo-quadrate) Lower jaw (Meckel's cartilage)	
	B. Second arch hyoid	Hyomandibular (suspensorium) Ceratohyal	Connected in middle line by the basihyal.
	C. Five branchial arches, each composed of :—	Pharyngeo-branchial Epibranchial Cerato-branchial Hypobranchial	Connected in middle line by the basibranchial.

Development.—The mandibular arch is first seen as two curved rods of cartilage, one on each side, lying in the hinder margin of the mouth and meeting in the mid-ventral line; each later splits into upper and lower jaws. The hyoid arch arises in a similar manner in the septum between the spiracle and the first gill cleft, but the rods do not meet in the middle line. Its upper end soon acquires an articulation with the auditory capsule, and later it splits into two. The branchial arches also arise as two half hoops of cartilage in the

septa between the gill slits, which segment first into two and then into four pieces on each side. The basihyal and basibranchial are separately developed.

Appendicular Skeleton.

The remaining part of the skeleton consists of the supports of the median fins, the paired fins and the girdles supporting the latter.

The dorsal fin is composed of two morphologically distinct parts; firstly, endoskeletal structures known as **pterygiophores** or **somactidia**, and secondly, exoskeletal structures, the **dermotrichia.** The somactidia take the form of a series of cartilaginous rods (12 in the first dorsal fin), attached to a corresponding number of neural spines. Each rod consists of a short basal element, these tend to fuse to form **basalia,** and a distal longer piece, the **radialium,** bearing at its extremity two polygonal plates. To these plates are attached a number of dermotrichia, which are horny fibres lying in the dermis and constituting the support of the main part of the blade of the fin. The ventral fin is somewhat similar in build, but the cartilaginous elements are reduced, while in the caudal fin they disappear altogether, leaving the dermotrichia to be borne directly by the neural and hæmal spines which are greatly enlarged in this region.

The pectoral girdle consists of a strong hoop of cartilage, irregular in shape and incomplete dorsally, lying embedded in the muscles of the body wall a short distance behind the last gill arch. The median part forms a fairly straight bar running transversely and expanded slightly in the centre to form a thinner plate which passes forward a little to form a platform supporting the hinder end of the floor of the pericardial cavity. This may be termed the coracoid portion of the girdle, and in reality it consists of two bars, as is clearly shown in its development, corresponding with the coracoids of *Rana*, but they have met in the middle line without the intervention of a sternum and fused so as to lose their individuality. The laterial extremity of the bar is marked on each side by three smooth articular surfaces on its posterior aspect which bear the proximal cartilages of the pectoral fin. The remaining parts of the girdle, the scapular portions, are horn-shaped, curved tapering rods passing dorso-mesially to end in the muscles on each side of the vertebral column.

The basalia of the pectoral fin, as has been noted, are three in number, representing the fusion of a series of somactidia. They increase markedly in size from before backwards, and are known as the **pro-, meso-** and **meta-pterygium** respectively. Following these are a series of about 16 radiala, which again terminate in

polygonal plates. To these are attached a large number of dermotrichia, giving the characteristic outline to the fin.

The pelvic girdle is a more simple structure, and consists of one more or less straight bar of cartilage running transversely in the muscles of the body wall, immediately in front of the cloaca. Its postero-lateral corner is hollowed to form an articular facet that bears the pelvic fin, while antero-laterally it is produced forward in a short bluntly pointed process.

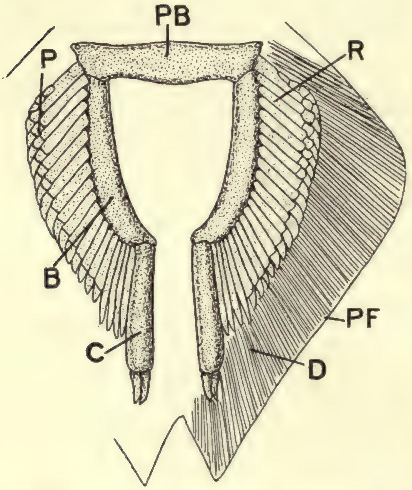


FIG. 72.—Pelvic girdle and fin of *Scyllium*.

B., basipterygium; C., skeleton of clasper; D., dermotrichia; P., polygonal plates; P.B., pelvic bar; P.F., pelvic fin; R., radialia.

The fin skeleton is also simpler, the somactidia having fused to form a single basalium, termed the **basipterygium.** This bears a series of radialia, terminating in polygonal plates, and these in turn carry the customary dermotrichia. In the male fish the innermost radialium is greatly enlarged, grooved on its dorsal surface and constitutes the skeleton of the clasper.

We have seen, then, that the structure of all the fins is essentially the same, they are indeed homologous. Furthermore, it is fairly clear that the median fins have been evolved from one long continuous fin running along the back, around the tail and forward ventrally to the anus, for we find such a fin not only in such forms as *Amphioxus*, and the lowly Cyclostomes, but also in the embryos of some fish and in the tadpole. This long fin has been split up probably in response to the needs of stability and locomotion, and has been developed at the points of the greatest mechanical advantage, while the intervening portions have been suppressed. The origin of the paired fins is not so obvious, but is a matter of interest. A theory known as " the lateral fold theory " is perhaps the most generally held. According to this the ancestral fish form had a lateral fold of skin running forward from the cloaca to the region of the gill clefts, somewhat similar to that found in *Amphioxus*. Like the median fin, these lateral folds were developed at some points and suppressed over the remainder. A fair amount of evidence supports this point of view. Thus in *Cladoselache*, a fossil shark

from the Devonian rocks, we find the pectoral and pelvic fins are similar in shape to the dorsal fins of *Scyllium, i.e.* very broad at the base and lying parallel with the long axis of the body. The radialia of the pelvic fins are just simple rods of cartilage with their bases embedded in the muscles of the body wall, but those of the pectoral show signs of fusion at their bases. In some embryos a very similar stage is passed through, and the two fins are even joined by a low ridge of skin. The girdles are thought to have originated by a further fusion of the somactidia, their sinking lower into the muscles of the body wall and, finally, in order to form an efficient mechanical support for the movement of the fin, extending markedly in a direction transverse to the long axis of the fish, with the consequent development of an articulation between fin and support. Observations on the development of the paired fins, particularly with regard to their muscle supply, also go to prove that they represent the concentrations of fins that were originally joined to the body by a very much longer base than at present.

CHAPTER IX

SCYLLIUM CANICULA—(*continued*)

Alimentary system—Respiratory system—Circulatory system—Urogenital system.

Alimentary System.

The digestive system consists of a long canal running from mouth to anus, mainly in the cœlom, and it is about twice as long as the distance between these two points. Certain glands are connected with this canal as in the frog, and they play important rôles in the digestive processes.

The crescentic mouth leads into a fairly capacious oral or buccal cavity whose walls possess no salivary glands, and in the floor of which the basihyal cartilage forms a low projection, having almost the appearance of a tongue, although it cannot be considered as such an organ. The whole cavity, being developed as a stomodœum, is lined with ectoderm, and owing to this fact is able to bear the teeth. It has been pointed out previously that the teeth are homologous with the denticles covering the skin, and, indeed, in the embryo they are in a continuous sheet with them, not being separated until later by the formation of a scaleless lip groove. The teeth are borne in a series of parallel lines over the jaws, in which they are not embedded, but to which their bases are attached by a very tough fibrous tissue. As all are similar in structure, and not different from one another like our own, the dentition is said to be **homodont**. Also, since there are a number of rows, indeed, as fast as the outer row wears out a new row takes its place, we find a number of successions of teeth, a condition termed **polyphyodont.** This stands in marked contrast to ourselves, where but two sets are fully developed, the milk teeth and the permanent teeth, that is, a **diphyodont** condition.

The hinder end of the roof of the buccal cavity bears a small transverse fold of skin, the **oral valve,** otherwise the cavity passes over imperceptibly into the pharynx. There is a noteworthy morphological difference between the two regions, however, since the pharynx is lined by entoderm and constitutes the beginning of the **mid-gut** or **mesenteron.** The pharynx is a fairly short flat tube for the passage of the food, but being mainly concerned with the function of respiration, and its ventro-lateral walls are marked by

the presence of the internal spiracular opening and five long narrow slits, the **internal branchial clefts.** Each cleft leads into a branchial pouch, also lined with entoderm, the anterior and posterior walls of which, with the exception of the hinder wall of the last, are thrown into the branchial folds or filaments. The tissue forming the partition between one pouch and the next constitutes the **inter-branchial septum**, in which lie the cartilaginous rods of the branchial skeleton and the blood-vessels of the gills. One septum with its skeletal and vascular elements and the branchial filaments on each side of it is termed a complete gill or **holobranch**, so that we find on each side of the fish four complete gills. The filaments on one side of the pouch form a half gill or **hemibranch,** so that in addition to the four holobranchs there is also on each side of the front wall of the first gill pouch a single hemibranch. The pseudobranch already noted on the anterior wall of the spiracle is, therefore, to be regarded as a spiracular hemibranch which, however, is vestigial and without functional significance. Movements of the branchial region take place during respiration, whereby the water is kept circulating over the highly vascular filaments, which are thus kept supplied with oxygen. The movements are brought about by a fairly complex series of muscles connected with the branchial basket.

Behind the gill clefts the pharynx passes over into a somewhat narrower tube, the œsophagus, which possesses dark-coloured walls owing to the presence in them of a rich plexus of capillaries, and is quite short. It is lined by a characteristic stratified epithelium.

The œsophagus leads into the stomach, and the transition from one to the other is marked on the outside by a change in coloration, and on the inside by an alteration in the character of the mucosa, which becomes a simple columnar epithelium of a highly glandular nature. The stomach is a large U-shaped tube, whose proximal, wider end lying to the left is termed the **cardiac portion.** The distal, somewhat narrower end on the right is known as the **pyloric portion**, and it runs forward again parallel with the cardiac portion almost to the level of the œsophagus, where it turns back upon itself to form a short swelling, the **pyloric enlargement,** followed by a marked constriction, the **pylorus.** The structure of the stomach wall is on the whole very similar to that in *Rana*, and its circular muscle fibres are very strongly developed in the region of the pylorus to form the **pyloric sphincter,** a circular constrictor muscle. Internally when the stomach is empty, or only moderately full, the mucosa is thrown into a series of longitudinal folds which disappear when the organ is distended. Inside the pylorus is a ridge of the mucosa termed the pyloric valve which, when the sphincter contracts, enables the stomach to be shut off from the intestine while the food undergoes

the initial changes of the digestive processes. The dogfish is a voracious feeder, so that the stomach is often full or even much distended with food, and it frequently contains in addition an enormous number of parasitic worms.

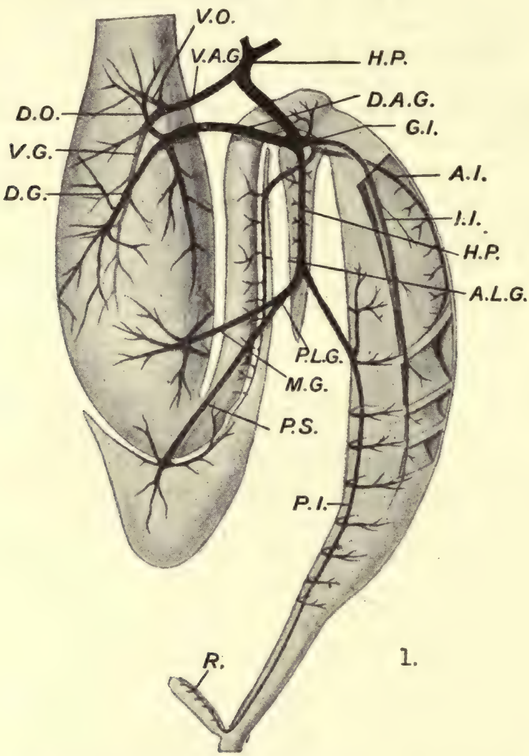


FIG. 73.—Sketch of the arrangement of the hepatic portal factors in *Scyllium*, seen from the dorsal side. The vessels were injected and the gut hardened and removed whole from the body-cavity.—After O'Donoghue.

A.I., anterior intestinal vein; *A.L.G.*, anterior lieno-gastric vein; *D.A.G.*, dorsal anterior gastric vein; *D.G.*, dorsal gastric vein; *D.O.*, dorsal œsophageal vein; *G.I.*, gastro-intestinal vein; *H.P.*, hepatic portal vein; *I.I.*, intra-intestinal vein; *M.G.*, median gastric vein; *P.I.*, posterior intestinal vein; *P.L.G.*, posterior lieno-gastric vein; *P.S.*, posterior splenic vein; *R.*, portion of posterior intestinal vein on the rectal gland; *V.A.G.*, ventral anterior gastric vein; *V.G.*, ventral gastral vein; *V.O.*, ventral œsophageal vein.

The intestine is composed of two parts, the intestine proper and the rectum. The intestine lies slightly to the right of the pyloric portion of the stomach, and has the form of a fairly wide spindle-shaped tube passing backwards to a point just behind the level of the bend of the stomach. Into its upper end open the pancreatic and bile ducts, and below this its wall is marked by more or less

circularly running blood-vessels. The intestine is characterised inside by the development of a very striking structure known as the spiral valve. It is a large fold of the mucosa twisted into a spiral form. Although in lower forms like the lamprey and in the embryo this is only a low fold recalling the typhlosole of the earthworm, save that it is spirally inserted in the gut wall, in the adult *Scyllium* it is a very wide fold. Its free edges have united in the middle of the intestinal lumen to form a spirally twisted median axis, and so the cavity, instead of being more or less straight, is converted into a fairly narrow spiral of about eight complete turns. If the wall of the intestine be cut, it presents the appearance of a series of imperfect slightly truncated cones with their bases directed backwards and fitting one inside the other. Thus, although the intestine is relatively short, the path actually traversed by the food in passing through it is quite long. Like the typhlosole, this arrangement has two results ; firstly, it retains the food within the gut for a much longer time to enable digestion to be completed, and, secondly, it provides a much larger area over which the food can be absorbed. The same ends are attained in the higher vertebrates by the development of a long, much-coiled intestine. The beginning of the rectum, just behind the level of the bend of the stomach, is marked by the presence of a small reddish club-shaped structure, the **rectal gland,** attached to its dorsal wall. This body is highly glandular, and has a central duct opening into the beginning of the dorsal wall of the rectum. The function of this rectal gland has not yet been ascertained satisfactorily, but it is probably the homologue of the cœcum of the higher animals, so that the intestine in front of it corresponds to the small intestine of those forms, and all there is to represent the large intestine is the rectum. In the dogfish the rectum runs straight on into the cloaca, into which also open the excretory and reproductive ducts, as has been pointed out previously.

The histology of the various parts of the alimentary canal is on the whole similar to that of the frog. In the connective tissue underlying the enteric epithelium are situated a number of small nodules of lymphoid tissue, each enclosed in a fairly definite capsule and known as the **lymph follicles.**

In addition to the rectal gland there are connected with the alimentary canal two glands that play important parts in digestion, these are the liver and the pancreas. The liver is a large conspicuous dark brown gland divided up into two main lobes, one on each side of the body, and a much smaller middle lobe lying ventral to the stomach. The three lobes are continuous at the anterior end and bound together and held in position by a strong membrane, the **suspensory ligament** of the liver, which attaches them firmly to the

membrane separating the pericardial from the peritoneal cavities. The liver is composed of a large number of ramifying branched tubules, which, as they originate from an outgrowth of the alimentary canal, are of entodermal origin and so constitute a compound tubular gland, although the actual structure of the adult gland is masked by its being tightly bound together by mesodermal connective tissue. Embedded in the front end of the left lobe of the liver is a fairly large thin-walled sac of dark green colour, the gall bladder, in which is stored the bile secreted by the liver. From it comes off a small tube, the **cystic duct,** which runs between the two main lobes for a short distance, receiving from them several smaller **hepatic ducts.** After the confluence of these, the main tube, now distinguished as the **common bile duct,** runs on to open into the ventral side of the intestine a short distance beyond the pylorus and behind the beginning of the fold of the spiral valve. The liver of *Scyllium* has the same complex functions as it has in *Rana.*

The pancreas is a long thin body of a yellowish-white colour and triangular in cross section, lying dorsally to the intestine and pyloric portion of the stomach. At the front end it expands into a small ventral lobe which lies tucked in the bend between the stomach and intestine close to the pylorus. The pancreatic duct runs through the substance of the gland, emerges from the posterior corner of the ventral lobe, enters the intestinal wall below the pylorus, and after running in the wall of the intestine for about half an inch opens into the inside close to the beginning of the spiral valve near the aperture of the bile duct. Like the liver, the pancreas arises as an outgrowth of the alimentary canal, and so is composed of entodermal cells grouped in glandular acini and bound together by mesodermal tissue. Its function is similar to that of the frog.

Another quite conspicuous very dark glandular-looking mass is attached to the posterior border of the stomach in the form of a U. This is the spleen, and it is not connected functionally with digestion nor developmentally with the alimentary canal, but is mentioned here because it is bound to the stomach by a strong fold of the mesentery.

From the last part of the œsophagus to the end of the rectum the gut lies more or less freely in the cœlom, but is held in position by a reflection of the peritoneum lining the cœlomic cavity. In the embryo this fold is complete from end to end and is known as the **dorsal mesentery,** since it comes off from the mid-dorsal line of the cœlom. The posterior middle portion of this disappears in the adult, leaving a large anterior part, the **mesogaster,** supporting the stomach and first half of the intestine and a smaller posterior part, the **mesorectum,** attached to the rectum and rectal gland. These

folds are generally spoken of as mesenteries, and they give rise to a series of lateral peritoneal folds which hold the other viscera in position ; such side folds are termed omenta and receive their name from the organs they surround. Thus we can recognise a **gastro-hepatic omentum** connecting liver and stomach, in this run the bile duct and portal vein ; a **gastro-intestinal omentum,** binding stomach and intestine ; and a **gastro-splenic omentum,** joining the spleen to the stomach.

Respiratory System.

The anatomy of the respiratory system has already been considered in dealing with the alimentary canal, since the respiratory organs, the gills, are derived from modified outgrowths of the walls of the pharynx. All the blood leaving the heart is taken to the gills by a series of vessels, collected up by another set and then conveyed all over the body. In the tiny filaments the vessels break up into numerous small capillaries, thus allowing the blood to be brought quite close to the surrounding water. This water is constantly being changed by the action of the branchial muscles, and so the oxygen contained in it is able to pass into the blood, and at the same time the carbon dioxide in the latter can pass out into the water by diffusion. Unlike the frog, respiration is limited to this region and not carried on over the general surface of the body.

Circulatory System.

The circulatory system in *Scyllium* is in some ways similar to that of *Rana*, but it is of a more primitive type and is of interest in comparative morphology, as the main outlines of its general plan are encountered in the embryos of all the higher Craniates. It is composed of a blood-vascular system and a lymphatic system. The blood-vascular system is a closed one as in all Craniates, and consists of a heart, arteries, capillaries and veins which form one series of closed vessels not communicating with the outside. As in the frog, some of the fluid plasma of the blood oozes through the walls of the capillaries to bathe the various tissues, and this is collected up by the lymphatic vessels and returned to the blood again. Owing to the difficulty of finding the lymphatic vessels, particularly in *Scyllium*, by the ordinary methods of dissection the term " circulatory system " is often employed to mean the blood-vascular system only.

Heart.

The heart is a stout muscular organ the rhythmic contraction of whose walls produces the difference in pressure necessary to keep the blood circulating, and so it forms the centre

of the system. It lies in a triangular space, the **pericardial cavity,** situated behind and beneath the last pair of gill pouches and so occupies a position underneath the hinder end of the pharynx. This is the primitive place for the heart, much further forward than in *Rana*, and indeed in what would be the neck region of the higher animals. In the embryo the pericardial and peritoneal cavities are in open communication with one another, but they become separated at quite an early date by the formation of a septum. This septum completely cuts off the two cavities, and hence, as it forms the posterior limit of the heart chamber and the anterior wall of the abdominal cœlom, it is termed the **pericardio-peritoneal septum.** Before the adult condition is reached a secondary tubular outgrowth, the **pericardio-peritoneal canal,** grows backwards from the postero-dorsal corner of the pericardial space, putting the two cavities in communication with one another again. The posterior part of the floor of the pericardial cavity is formed by the median extension of the coracoid bar and its roof by the basibranchial cartilage. The cavity itself is lined by peritoneum, which is also reflected to form a smooth visceral layer that closely invests the heart and is known as the pericardium.

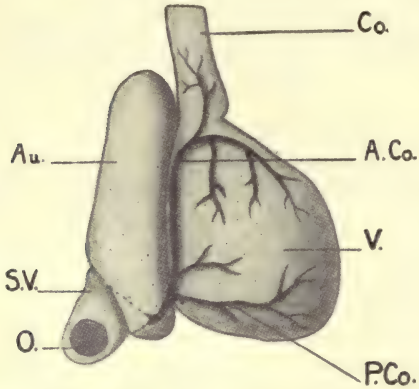


FIG. 74.—Lateral view of the heart to show the arrangement of the coronary veins. —After O'Donoghue.

A.Co., anterior coronary vein; Au., auricle; Co., conus arteriosus; O., opening of ductus Cuvieri; P.Co., posterior coronary vein; S.V., sinus venosus; V., ventricle.

The heart itself is composed of four chambers and may be considered as starting at the hinder end of the pericardial cavity by the running together of two large veins, the ductus Cuvieri, from the postero-lateral corners of the cavity to form the **sinus venosus.** This, the first part of the heart, is a large thin-walled tubular sac lying transversely to the long axis of the body, continuous laterally with the ductus and attached to the pericardio-peritoneal septum by its posterior border. It opens by a single median aperture into the postero-dorsal border of the single large **auricle** or **atrium,** the opening being guarded by a membranous sinu-auricular valve. The auricle is a triangular muscular sac with its apex directed forward,

its lateral corners produced into small lappets, the auriculæ, and it is situated in the dorsal part of the pericardial cavity. This chamber communicates with the ventricle in the middle of its postero-ventral border by a transverse slit guarded by a pair of auriculo-ventricular valves. The **ventricle** is a very thick-walled muscular flask-shaped structure on the ventral side of the pericardial cavity, and so it forms the most obvious part of the heart when dissecting the fish from the ventral side. The neck of the flask, as it were, is continued forward as a thick muscular tube, the **conus arteriosus,** which passes up to the ventral corner of the apex of the pericardial space, outside which it is continued as a median artery, the **ventral** or **cardiac aorta.** Inside the conus are two rows of semilunar valves, each composed of three watch-pocket like flaps, the proximal row separating it from the ventricle. The conus is actually part of the heart, being composed of the same cardiac muscle fibres that distinguish the ventricle and taking part in the waves of contraction that pass over the heart. The object of all the valves in the heart is to keep the blood flowing in the same direction by preventing regurgitation when the pressure behind it is released.

It will be seen from the above description that the heart is in reality a single tube, and its development shows that it originates as the specialisation of a part of a median ventral vessel. The heart of all vertebrates arises similarly as a single tube, which later becomes bent upon itself in the form of an S. In *Scyllium* the heart is interesting because it always remains in this primitive condition, and its folded nature can be demonstrated very easily if it be removed from the pericardium and cut in median longitudinal section.

Arterial System.

The vessels conveying the blood from the heart to the various parts of the body constitute the arterial system. All the blood leaves the conus by the one great trunk, the ventral aorta, which runs forward below the hypobranchial elements giving off paired branches, the **afferent branchial arteries,** to the gills. The ventral aorta passes forward to the lower ends of the ceratohyal cartilages to a spot immediately behind the thyroid gland, and there bifurcates into two branches, the **innominate arteries,** which turn directly laterally. After a very short course each innominate divides into two ; the first afferent branchial artery which runs along the hyoid arch and supplies the first hemibranch, and the second afferent branchial which runs along the first branchial arch and feeds the posterior hemibranch of the first gill pouch and the anterior hemibranch of the second pouch, in other words the first complete gill. The third afferent branchial artery arises about half-way back to the

conus, and runs outwards on the second gill arch serving the second holobranch. The fourth and fifth afferent branchials are given off almost together just outside the pericardium, and running on the corresponding gill arches supply the next two holobranchs. The afferent branchials break up into a rich capillary plexus in the gill filaments, so enabling the blood to give up its carbon dioxide and take up oxygen.

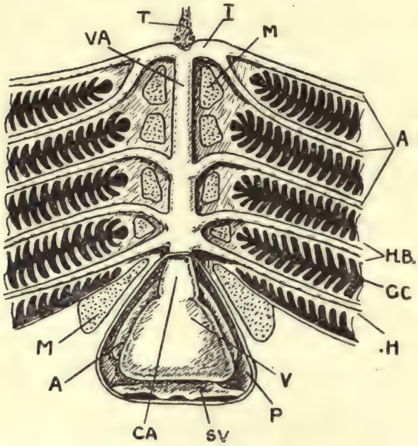


FIG. 75.—Ventral aorta and afferent branchial arteries of *Scyllium*.

A., auricle; A.B., afferent branchial arteries; G.C., gill cleft; H., hemibranch; H.B., holobranch; I., innominate artery; M., muscles; P., pericardium; S.V., sinus venosus; T., thyroid gland; V., ventricle; V.A., ventral aorta.

The oxygenated blood from the gills is collected up by **efferent branchial arteries,** vessels running the complete length of each hemibranch. The first eight on each side are joined at each end so as to form complete loops around the first four gill pouches, and this leaves a single vessel along the anterior hemibranch of the fifth pouch, none being required along its hinder edge as it bears no gill filaments. These loops are joined about half-way along their length, *i.e.* laterally, by short longitudinal trunks passing across the gill arches, and by means of the last of these the hindermost and incomplete half loop drains into the preceding loop. From the inner, dorsal ends of the loop come off four pairs of **epibranchial arteries** which pass backwards and inwards in the sub-mucosa of the dorsal pharyngeal wall to unite in the middle line and form the **dorsal aorta,** which is the main big visceral artery and runs back to the end of the tail.

Three arteries form the main source of supply for the head region. A slender **mandibular artery** is given off from the extreme ventral corner of the first efferent branchial loop, and this passes forward to the muscles of the lower jaw and also the hyoidean region. From the middle of the first efferent branchial, *i.e.* in line with the longitudinal trunks, arises a fair-sized vessel variously termed the **hyoid,** the **anterior** or **ventral carotid artery,** which runs forward dorsal to the hyomandibular cartilage and in the anterior wall of the spiracle. It goes on across the floor of the orbit and

enters the cranium by a foramen whose position we have already seen. The third vessel, the **common** or **dorsal carotid artery,** takes its origin from the dorsal end of the first efferent loop right beside the first epibranchial artery. It curves forwards and inwards in the sub-mucosa of the roof of the pharynx to a point about level with the spiracle. Here it receives an anastomosing trunk from the

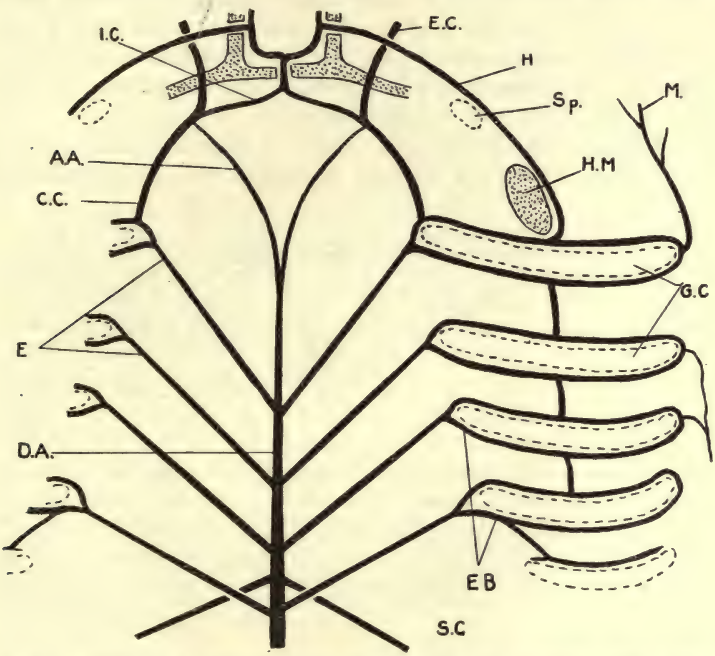


FIG. 76.—Diagram of efferent branchial arteries of *Scyllium*, seen from the ventral side with the left half of the lower jaw and floor of mouth stretched out and the right half cut off.

A.A., anterior prolongation of aorta; C.C., common carotid; D.A., dorsal aorta; E., epibranchial artery; E.B., efferent branchial; E.C., external carotid; G.C., gill cleft; H., hyoidean artery; H.M., hyomandibular cartilage; I.C., internal carotid; M., mandibular artery; S.C., sub-clavian; Sp., spiracle.

dorsal aorta; the aorta itself passes forward from the union of the first pair of epibranchials as a small trunk which bifurcates at the level of the first gill cleft, its two ends bending outwards to run into the common carotids. Immediately beyond this the common carotid divides into two, a slender **internal** or **posterior carotid artery** and a stouter **external carotid.*** The former trunk passes inwards to the

* The naming of these anterior arteries, particularly the carotids, is not satisfactory, as their homologies with the arteries of the higher animals have not yet been accurately determined.

mid-ventral line, where it penetrates the floor of the cranium with its fellow, through the carotid foramen just behind the pituitary fossa. The external carotid artery runs forward and out through a small foramen into the orbit, passing outwards below the maxillary branch of the fifth cranial nerve to supply the muscles of the eye, the upper jaw and the snout.

The hinder parts of the body are all supplied by branches coming directly from the dorsal aorta. The first noticeable one of these, the **sub-clavian artery,** arises just in front of the fourth epibranchial artery and runs outwards and backwards under the dorsal peritoneum of the cœlom to the pectoral girdle and fin.

A short distance behind this arises a large median vessel, the **cœliac artery,** which runs out into the cœlom in the mesogaster just

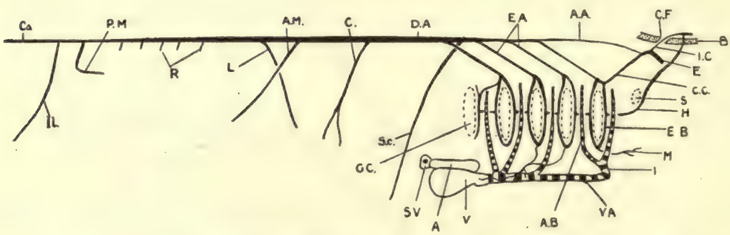


FIG. 77.—Lateral view of the arteries of *Scyllium.*

A., auricle ; A.A., anterior extension of dorsal aorta ; A.B., afferent branchial artery ; A.M., anterior mesenteric artery ; B., basal region of cranium ; C., cœliac artery ; Ca., caudal artery ; C.C., common carotid artery ; C.F., carotid foramen ; D.A., dorsal aorta ; E., external carotid artery ; E.A., epibranchial artery ; E.B., efferent branchial artery ; G.C., gill cleft ; H., hyoidean artery ; I., innominate artery ; I.C., internal carotid artery ; Il., iliac artery ; L., lieno-gastric artery ; M., mandibular artery ; P.M., posterior mesentric artery ; R., renal arteries ; S., spiracle ; S.C., sub-clavian artery ; S.V., sinus venosus ; V., ventricle ; V.A., ventral aorta.

dorsal to the stomach and divides into two branches ; the one supplies the anterior end of the stomach and the liver, while the other serves the front end of the intestine and the pancreas.

Two further median trunks take their origin quite close together about an inch and a half further back ; these are the **anterior mesenteric** and the **lieno-gastric arteries.** The former goes backwards to supply the posterior part of the intestine and the gonads, and the latter runs forward, thus crossing the anterior mesenteric, and is distributed to the posterior bend of the stomach, the spleen and also part of the pancreas.

The next median vessel to come off from the aorta is a smaller one, the **posterior mesenteric artery,** which runs through the meso-rectum mainly to the rectal gland. Thus there are four large splanchnic arteries running to the gut in the place of the large cœliaco-mesenteric and small posterior mesenteric arteries present

in the frog, owing to the great shortening of the body region that has taken place in the forms ancestral to *Rana*.

Behind this, again, we find the small paired **iliac** or **pelvic arteries** related to the pelvic girdle and fins. After this the dorsal aorta, now considerably reduced in size, enters the hæmal arches of the caudal vertebræ and runs in them to the end of the tail.

In addition to these more obvious vessels the dorsal aorta also gives off a series of small paired **parietal arteries,** one pair to each muscle segment of the body, and again in the region of the functional part of the kidney a number of paired **renal arteries.**

Before leaving the arterial system it will be as well to glance briefly at the development of its most interesting part, namely, the afferent and efferent arteries. In the early embryo with the gill slits laid down, but before the gill filaments are developed, we find coming off from the ventral aorta six pairs of vessels which pass as uninterrupted arches, the **aortic arches,** around the pharynx in the corresponding gill bars, the first one lying in the hyoid arch. On the dorsal side of the pharynx the six arches on each side run into a separate longitudinal trunk, so that there are at this time two dorsal aortæ running the length of the body which do not fuse to form a single vessel until later. This is a very important stage from the point of view of comparative anatomy, since it persists in the pharyngeal region of the adult *Amphioxus* and is also met with in a more or less modified condition in the embryos of all the higher animals, ourselves included. At a later stage the hyoid arterial arch degenerates, and with the development of the gill filaments the originally continuous arches become split, so giving rise to the afferent and efferent branchial arteries.

Venous System.

The most striking feature in the venous system is the manner in which a number of the main vessels have become dilated. They have lost their definite walls and spread out to form very irregular spaces termed sinuses, whose relations to other veins are sometimes difficult to make out. For descriptive purposes it is convenient to divide the veins into the anterior, those in front of the heart, and the posterior, those behind.

Anterior Veins.

A very distinct channel runs from the snout back to the heart on the dorsal side of the fish. This commences as a well-marked crescent-shaped **nasal sinus** which lies on the postero-mesial side of the olfactory organ. It communicates by means of a small **orbito-nasal vein,** which passes through the cartilaginous hinder

wall of the capsule, with the large **orbital sinus.** The latter is a large expansion occupying the whole of the cavity of the orbit not taken up by the eyeball and its muscles, and it receives towards its antero-mesial end a small **anterior cerebral vein** coming through the cranial wall from the front end of the brain. The two orbital sinuses communicate with one another by means of an **interorbital vein** which runs in the basicranial cartilage just behind the level of the pituitary body and opens into the orbit by a foramen just in front of and below the foramen for the main branches of the fifth and seventh and the sixth cranial nerves. The orbital sinus is continued backwards as the **post-orbital sinus** lying in the gutter-like post-orbital groove which, as we have seen, lies on the side of the auditory capsule below the ridge marking the horizontal semi-circular canal and the articular surface for the hyomandibular cartilage. In its course along the post-orbital groove the sinus receives the **posterior cerebral vein,** an important vessel leaving the cranial cavity in company with the tenth cranial nerve. Behind the skull the venous trunk enlarges to form the **anterior cardinal sinus,** a large irregular sinus situated along the internal dorsal ends of the gill clefts. The pharyngeo-branchial cartilages project into its floor, and the branchial branches of the vagus nerve pass freely through its cavity. At its posterior end behind the last gill cleft this sinus narrows considerably, and opens into the posterior cardinal sinus through an opening guarded by a valve.

A small vessel, the **inferior jugular sinus,** commences just behind the symphysis of the lower jaws and runs backwards to the level of the thyroid gland, where it communicates with its fellow by an irregular anastomosis that surrounds the gland. From this point it enlarges and becomes irregular, passing along the inner ventral ends of the gill clefts and then along the pericardium, finally opening into the ductus Cuvieri by a common opening with the sub-clavian vein just outside the limits of the pericardial space.

At the level of the thyroid gland a well-marked **hyoidean sinus** leaves the side of the inferior jugular and passes out laterally in a shallow groove in the external side of the hyomandibular cartilage. It runs round parallel with the first gill cleft to open into the hinder end of the post-orbital sinus, thus putting the dorsal and ventral vessels in communication.

Posterior Veins.

The blood is brought back from the tail by the **caudal vein,** which runs in the hæmal canal accompanying and ventral to the caudal artery. It leaves the canal and divides into two **renal portal veins** that pass up the dorso-lateral edges of the kidneys, to

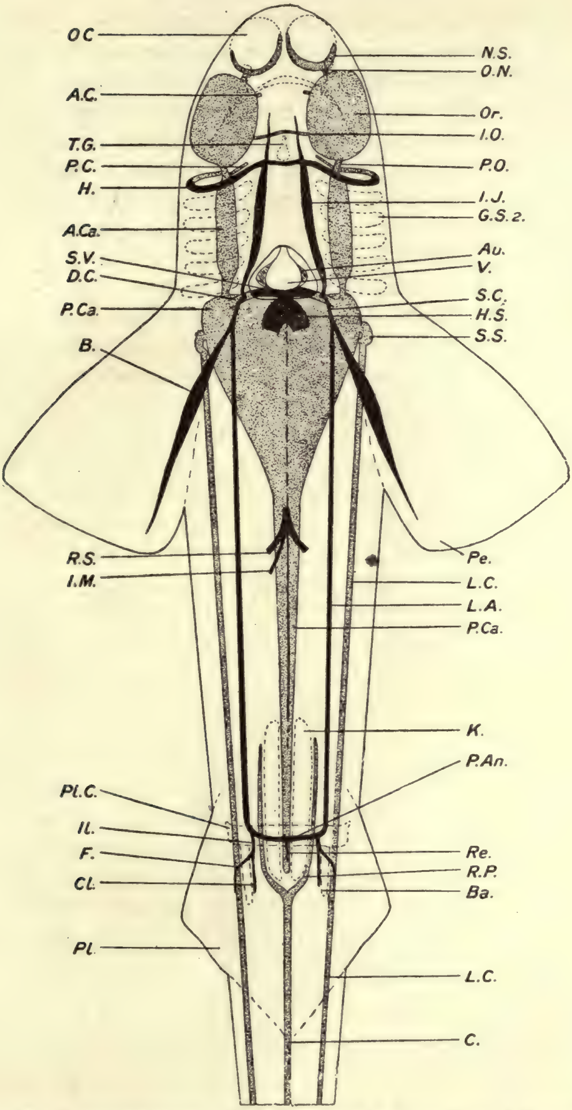


FIG. 78.—Venous system of *Scyllium canicula*.—After O'Donoghue.

Diagram showing the general disposition of the main venous trunks in *Scyllium canicula*. The more dorsally situated vessels are stippled and the more ventral ones black. For the sake of clearness, the ventral cutaneous vein has been omitted. *A.C.*, anterior cerebral vein ; *A.Ca.*, anterior cardinal sinus ; *Au.*, auricle ; *B.*, brachial vein ; *Ba.*, basipterygium ; *C.*, caudal vein ; *Cl.*, cloacal vein ; *D.C.*, ductus Cuvieri ; *F.*, femoral vein ; *GS2.*, 2nd gill-cleft ; *H.*, hyoidean sinus ; *H.S.*, hepatic sinus ; *I.J.*, inferior jugular sinus ; *Il.*, iliac vein ; *I.M.*, intestino-mesenteric vein ; *I.O.*, inter-orbital vein ; *K.*, caudal mesonephros ; *L.A.*, lateral abdominal vein ; *L.C.*, lateral cutaneous vein ; *N.S.*, nasal sinus ; *O.C.*, olfactory capsule ; *O.N.*, orbito-nasal vein ; *Or.*, orbital sinus ; *P.An.*, pelvic anastomosis between the two L.A. ; *P.C.*, posterior cerebral vein ; *P.Ca.*, posterior cardinal sinus ; *Pe.*, pectoral fin ; *Pl.*, pelvic fin ; *Pl.C.*, pelvic cartilage ; *P.O.*, post-orbital sinus ; *Re.*, rectal vein ; *R.P.*, renal portal vein ; *R.S.*, right spermatic vein ; *S.C.*, sub-clavian vein ; *S.S.*, sub-scapular vein ; *S.V.*, sinus venosus ; *T.G.*, thyroid gland ; *V.*, ventricle.

which they give off numerous **afferent renal** branches and getting smaller and smaller disappear at the anterior end of these bodies, into which all their blood is poured. Between the kidneys the **posterior cardinal sinuses** take origin as a median unpaired trunk formed by the running together of a number of **efferent renal veins.** The median trunk, however, is completely separated into two by a membranous septum as it passes forward from the front end of those glands under the peritoneum on the dorsal side of the cœlom. About half-way forward to the pericardio-peritoneal septum their partition disappears, and thereafter is only represented by a few bands of tissue. At the same point they receive a median genital sinus coming from the gonads, and in its turn receiving a vein from the right side of the intestine. The post-cardinal sinuses as they pass forward broaden out considerably until a little further on they occupy the whole of the dorsal width of the cœlom, and they reach as far as the pericardio-peritoneal septum. The blood from the muscles and skin on the dorso-lateral side of the fish is collected up by a **lateral cutaneous vein** which runs forward from the end of the tail under the lateral line in the septum between the epi- and hypaxial myotomes. At the level of the hinder end of the pectoral fin it dives down into the muscles and swells out to form a **sub-scapular sinus** lying on the internal lateral side of the scapular end of the pectoral girdle. This sinus opens into the antero-lateral edge of the post-cardinal sinus by an opening that is somewhat difficult to make out.

The blood from the pelvic fin and cloacal region is collected by a small **iliac vein** on each side and conveyed to the dorsal side of the pelvic cartilage, where it anastomoses with its fellow across the cartilage and continues forward as a distinct **lateral abdominal vein** in the ventro-lateral wall of the cœlom just beneath the peritoneum. It reaches the pericardio-peritoneal septum and turns sharply in it, dorsally and mesially along the posterior edge of the coracoid cartilage. A short distance along this it is joined by the large **brachial sinus** which comes in from the posterior border of the pectoral fin, and the trunk formed by the union of these two vessels is termed the **sub-clavian vein.** This vessel is a short trunk entering the ductus Cuvieri, as we have noted previously, by an opening common to it and the inferior jugular sinus.

Thus we have now accounted for the collection of the blood from all regions of the body save the alimentary canal, and this is dealt with, as in the frog, by a special **hepatic portal system** composed of a number of factors. It starts as a small vessel, the **rectal vein,** on the ventral side of the rectal gland, and this continues as the **posterior intestinal vein** up the dorso-lateral wall of the intestine to the level

of the hinder end of the pancreas. It then leaves the gut wall and, passing through the mesentery, enters the posterior corner of the gland, uniting as it does so with the **posterior lieno-gastric vein,** a trunk coming from the bend of the stomach and the spleen. In this way is constituted the main **hepatic portal vein,** which then runs up embedded in the dorsal edge of the pancreas to its anterior end, where it receives two large tributaries. The first of these is the **gastro-intestinal vein** formed by factors coming from the pyloric end of the stomach and the spleen adjacent thereto and the front end of the intestine and a fairly large **intra-intestinal vein** which lies right in the central axis of the spiral valve, and so is not readily seen save in a section. The second vessel is the **dorsal anterior gastric vein** formed in the main by the union of a branch from the dorsal side of the front end of the stomach and one from the œsophagus. The main hepatic portal vein now leaves the pancreas and runs through the gastro-hepatic omentum, where it is joined by a **ventral anterior gastric vein** of similar constitution to the dorsal vessel, but coming from the ventral side of the œsophagus. Finally it divides into right and left branches feeding the corresponding lobes of the liver.

The blood from the liver is taken up by two short **efferent hepatic veins,** one coming from the anterior end of each lobe of the liver. They almost immediately unite to form a large single **hepatic sinus,** which communicates with the ventro-posterior wall of the sinus venosus through the pericardio-peritoneal septum by two separate openings indicative of its double origin.

The **ductus Cuvieri** in the adult appears as a tube projecting a short distance into the post-cardinal sinus, wherein it opens by a spout-like aperture. It passes inwards on the ventro-lateral wall of the œsophagus through a conspicuous notch in the posterior border of the fifth cerato-branchial cartilage and on into the pericardial cavity, where it is continuous with the sinus venosus. Thus it will be seen it is the vessel by which the whole of the blood is returned to the heart, save only that brought from the liver by the hepatic sinus.

In the embryo the veins have not yet swollen up to form sinuses, so that their anatomical relationships are somewhat clearer. The anterior and posterior cardinal veins on each side join together at the level of the sinus venosus to form the ductus Cuvieri, and so both open into it. This, the primitive arrangement, is afterwards masked by the enormous enlargement of the two trunks so that, as noticed above, the anterior sinus opens into the posterior one and the ductus Cuvieri appears as a tube projecting into the latter. At a very early stage the anterior vein is one continuous vessel only, but at a somewhat later stage the part of it in front of the point

of entrance of the posterior cerebral vein is replaced by another vein, the lateral cephalic vein, which arises parallel with the front end of the old anterior cardinal, so that in the adult the vein is the result of the union of two vessels.

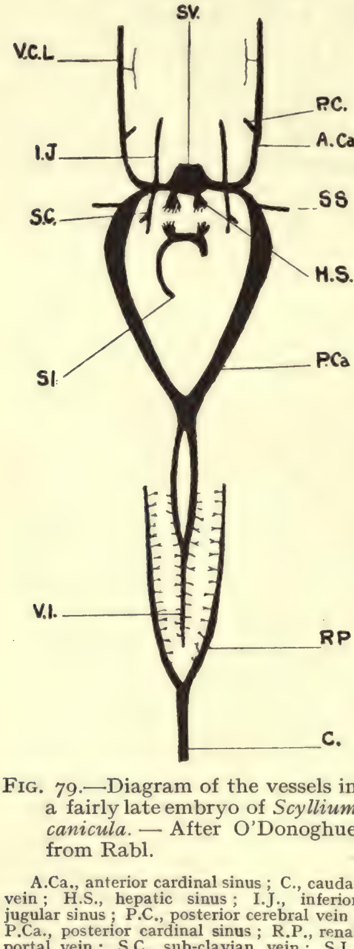


FIG. 79.—Diagram of the vessels in a fairly late embryo of *Scyllium canicula.* — After O'Donoghue from Rabl.

A.Ca., anterior cardinal sinus ; C., caudal vein ; H.S., hepatic sinus ; I.J., inferior jugular sinus ; P.C., posterior cerebral vein ; P.Ca., posterior cardinal sinus ; R.P., renal portal vein ; S.C., sub-clavian vein ; S.I., sub-intestinal vein ; S.V., sinus venosus ; S.S., sub-scapular vein ; V.C.L., vena capitis lateralis ; V.I., inter-renal vein.

At the beginning of their development the posterior cardinal veins are related to the first embryonic kidney and continuous with the caudal vein, but later, as in the frog, the posterior ends are split up by the growth of the mesonephroi. The hepatic portal system arises in a somewhat similar manner by the splitting of a primitive sub-intestinal vein.

The inferior jugular vein when developed opens into the middle of the front side of the ductus Cuvieri and the sub-clavian vein right opposite it.

In comparing the vascular system of *Scyllium* with that of *Rana* several fundamental differences are at once apparent. The heart in the fish has but a single atrium or auricle, whereas in the frog it is divided into two by an interauricular septum. Correlated with the development of the lungs we find that the primitive arrangement of the arteries, although represented in the tadpole, has undergone considerable modification. The blood in the dogfish can only travel in one direction, namely, first to the gills and thence to the body, so that we term this type of circulation, characteristic of fish in general, a **branchial circulation,** or, since there is only one stream leaving the heart, a **single circulation.** In the frog the blood may take one of two courses, it may go to the lungs and skin for aeration via the pulmo-cutaneous artery, or it may go to any other part of

the animal via the carotid or systemic arteries and back to the heart again. In spite of this double choice, however, the two blood streams returning to the heart, the aerated and non-aerated blood, are not kept absolutely separated in the ventricle, and thus we have an **incomplete double circulation.**

Urogenital System.

The excretory and reproductive organs are conveniently dealt with together, since they are closely related anatomically; indeed, the ducts of the reproductive organs are mainly derived from the primitive excretory ducts.

We may first consider the kidneys, since they are more nearly alike in the two sexes, but in order to understand the condition in the adult it is necessary to glance briefly at their development.

The kidneys arise, as in all Craniates, as tubular organs closely related to the myotomes or muscle segments. The first of these to develop are found in the early embryo towards the anterior end of the body cavity in the form of three or four tubules on each side in close proximity to the post-cardinal vein, and these constitute an imperfect excretory organ known as the **pronephros.** On the internal side each tubule possesses a ciliated funnel-shaped opening, the **nephrostome,** opening into the cœlom. This leads into a tube, only slightly coiled, lying in the thickness of the cœlomic wall, and a glomerulus such as we find in the kidney of *Rana* is either absent or only imperfectly represented. At their outer end these tubules run into a long duct, the pronephric or segmental duct, which passes in the body wall back to the cloaca. In *Scyllium* the nephrostomes fuse to form one opening. The pronephros is apparently never functional, and is probably to be regarded as the remnants of a body functional in ancestral forms. The tubules disappear in the adult, but the duct in some form or other is always to be found.

A short time after the pronephros makes its appearance, a second, much longer series of tubules, about twenty-nine in number, arises behind it. These tubules also have nephrostomes, but become more convoluted, and although at first they end blindly in the body wall, they soon acquire openings into the segmental duct. They constitute the second excretory organ, the **mesonephros** or **Wolffian body,** which soon acquires a duct for itself by a tube being split off from the pronephric duct. The tubules themselves increase in length, become highly convoluted and develop typical Malpighian bodies, so that they form active excretory bodies. These tubules are often described as the primary tubules in order to distinguish them from the secondary tubules, of which two or three arise, by budding from each primary tubule. The secondary tubules never develop nephrostomes,

and their appearance causes the mesonephros to increase markedly in size and they obscure its primitive segmental arrangement.

In the dogfish the secondary tubules are more numerous in the posterior half of the body, and both they and the primary tubules become much longer and more coiled, and in structure they are essentially like the urinary tubules in *Rana*. Then, too, they lose their direct connection with the mesonephric duct, and the collecting parts of certain tubules enlarge and form ducts that constitute secondary ureters. These open into the posterior part of the mesonephric duct in the female, or into one larger tube which only joins

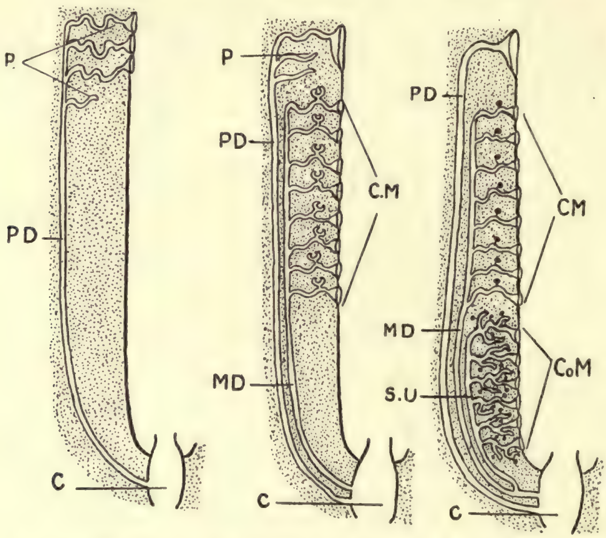


FIG. 80.—Diagram of development of kidneys of a female *Scyllium*.

C., cloaca; Co.M., caudal mesonephros; C.M., cranial mesonephros; M.D., mesonephric duct; N., nephrostome; P., pronephros; P.D., pronephric duct; S.U., secondary ureter.

the extreme end of the mesonephric duct in the male. Thus it is that the mesonephros in *Scyllium* becomes divided into two distinct parts, a head kidney or **cranial mesophros** and a much more substantial tail kidney or **caudal mesonephros,** often, but quite erroneously, called the metanephros, an entirely separate body developed only in the higher Craniata, the Reptiles, the Birds and the Mammals.

The kidneys of the adult, as we have seen, represent the persistent functional mesonephros of the embryo, and are divided into anterior and posterior moieties. They lie between the dorsal peritoneum and the muscles of the back, and so are outside the cœlom as in *Rana*. They lie partly embedded in hollows in the

muscles, and as the peritoneum covering them is quite thick they are not seen until it has been removed. The kidneys in the two sexes are fairly similar, so that they need not be dealt with separately.

The front end of the kidney in the female is very small and,

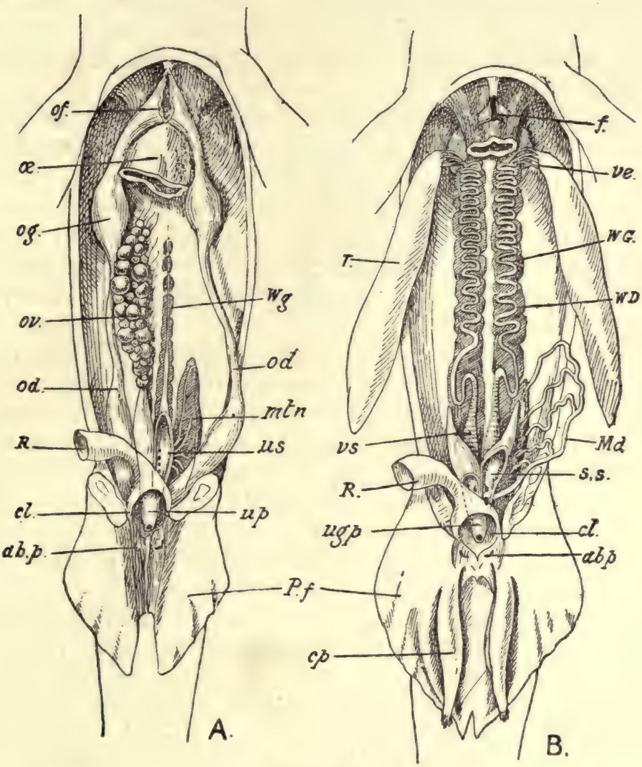


FIG. 81.

A., urogential system of the female; *B.*, urogenital system of the male dogfish; *ab.p.*, abdominal pores; *cl.*, cloaca; *cp.*, claspers of the male; *f.*, rudiment of the oviducal opening in the male; *M.d.*, metanephric ducts; *mtn.*, metanephros; *od.*, oviduct; *œ.*, cut end of œsophagus; *o.g.*, oviducal gland; *ov.*, ovary; *P.f.*, pelvic fins; *R.*, rectum; *s.s.*, sperm sacs; *T.*, testis; *u.p.*, urinary papilla in the female; *ug.p.*, urogenital papilla in the male; *u.s.*, urinary sinus; *v.e.*, vasa efferentia; *v.s.*, vesicula seminalis; *W.D.*, Wolffian duct; *W.G.*, Wolffian gland or mesonephros.

although perhaps retaining its excretory function to a certain extent, is so reduced that it may be considered almost vestigial. It presents the appearance of a series of small isolated patches of a brownish colour which increase slightly in size towards the hinder end. The posterior portion of the kidney is much larger, being wider and considerably thicker, and it forms one discrete body partially divided up into lobes.

While the caudal part of the mesonephros in the male is similar to that in the female, the anterior end is very different. It is larger than in the female, but almost completely hidden from view by the highly convoluted mesonephric duct that is closely applied to its ventral surface. In the embryo it is concerned with excretion, but in the adult this activity is lost and it is functional in secreting a nutritive fluid for the sperms, consequently it is sometimes termed the **epididymis.**

The mesonephric duct in the female is a straight fairly simple tube, commencing at the front end as a thin vessel which runs backwards on the ventral face of the kidney. In the hinder part it enlarges to form a **urinary sinus** into which open the secondary ureters, about six in number, and this unites with its fellow to constitute a small median urinary sinus opening upon the urinary papilla. The duct is concerned with the conveyance of urine to the exterior, so that it constitutes a ureter.

In the male the anterior portion of the mesonephric duct is much enlarged and bent upon itself. Into it opens the tubules, enlarged, devoid of Malpighian bodies and with their epithelium considerably modified. Near the line of demarcation between the cranial and caudal mesonephros the bends become fewer, and it passes on swelling out to form a seminal vesicle or **vesicula seminalis.** After receiving the urinary vessels at its lower end it unites with that of the opposite side to form a small median **urogenital sinus** whose opening is situated upon the urogenital papilla. The sinus on each side is produced into a forwardly directed long sac-like diverticulum, the **sperm sac,** which lies closely attached to the ventral surface of the seminal vesicle. The first four or five of the secondary ureters do not open into the mesonephric duct directly, as in the female, but into an accessory tube often termed " the ureter " which joins the seminal vesicle near its hinder end. Behind this, again, five or six secondary ureters draining the hinder extremity of the kidney open separately. These secondary ureters, the sperm sacs and the seminal vesicle, cover a large part of the ventral surface of the kidney. Thus it will be seen that in the male the mesonephric duct serves for the greater part of its length for the conveyance of the spermatic fluid, and so constitutes a **vas deferens,** and only the last part of it is concerned with the transference of urine.

In the female embryo an ovary starts to develop on each side, but that on the left soon disappears, so that in the adult we find only one ovary present, that of the right side. It is a conspicuous structure lying slightly to the right of the middle line along the median half of the cœlom, to the dorsal wall of which it is attached by a fold of peritoneum, the mesovarium. Its surface is marked

by numerous rounded projections, the ova, which are of different sizes from quite tiny knobs like pin-heads up to yellow spheres 14 mm. in diameter, according to their state of development. The pronephric tubules disappear, as has been pointed out, but the funnels of the two sides remain and, moving ventrally, unite below the œsophagus to form a single opening, the **oviducal funnel.** This communicates by means of one of the tubules with the segmental duct. Not merely does the pronephric duct persist, but it enlarges considerably and constitutes the oviduct of the adult. The oviduct is a thick-walled tube commencing at the funnel and passing laterally on to the latero-dorsal wall of the cœlom. A short way along it swells out to form a marked ovoidal enlargement, the **oviducal gland,** and then becomes constricted again. The walls of the posterior half of the duct are thin, and the cavity enlarged to form a hollow vesicle, the **ovisac,** in which the egg can be kept until laid. The two oviducts open to the exterior by a single median aperture on the dorsal wall of the cloaca, which in the young female is closed by a thin membrane, the **hymen.**

When ripe, the follicle ruptures and discharges the egg, now a spherical mass about 14 mm. in diameter and loaded with yolk, into the cœlom. It makes its way into the oviducal opening and passes into one oviduct—apparently the two oviducts function alternately. In the top end of the tube it is penetrated and fertilised by a sperm that has been introduced previously by the male fish, and it is also provided with an albuminous coat. As it passes the oviducal gland and beyond it is provided with a horny shell, the product of the secretion of the gland. The shell is an oblong purse-shaped structure with its long sides continued out as four horns tailing off as long coiled threads, by means of which it is anchored to the seaweed when laid. While in the oviduct the shell is of a pale yellow colour, but after the hatching of the young and subsequent exposure it turns black. Such empty cases belonging to *Scyllium*, or some other Elasmobranch, are commonly cast up on the seashore and are known as "mermaids' purses."

The segmental duct in the male is functionless, but always remains as a vestigial structure in the form of a tiny, almost invisible, solid strand of tissue in the position of the oviduct in the female. Traces of it may sometimes be seen in certain specimens.

The testes are two elongated, soft bodies lying one on each side of the middle line, and suspended from the dorsal wall of the cœlom by special folds of the peritoneum known as the mesorchia. Each testis is attached to the front end of the corresponding mesonephros by a number of fine tubules, the **vasa efferentia,** by whose agency the sperms produced in the seminiferous tubules of the testis are

conveyed to the modified urinary tubules, and thence to the mesonepheric duct. As has been noted above, this duct, functioning as a vas deferens, is a thick-walled, greatly-coiled tube lying on the ventral side of the mesonephros. The cranial mesonephric tubules secrete a nutritive fluid in which the sperms live. The semen, as this fluid with its contained sperms is termed, is probably stored in the vesicula seminalis until required for use.

For convenience in reference we may tabulate the relation between the embryonic and adult excretory ducts in the following manner :—

EMBRYONIC EXCRETORY STRUCTURES AND THEIR FATE IN THE ADULT.

Embryo.	Adult female.	Adult male.
Pronephros.	Disappears save for oviducal opening.	Disappears.
Pronephric duct.	Oviduct.	Vestigial.
Cranial mesonephros.	Of small functional significance.	Transformed into secretory tubules the "Epididymis."
Caudal mesonephros.	Functional kidney ; parts of the mesonephric tubules are converted into secondary ureters.	Functional kidney ; parts of the mesonephric tubules are converted into secondary ureters, one of which is very large.
Mesonephric duct.	Anterior end small, posterior end enlarged to form urinary sinus, whole functions as ureter.	Anterior end large, forms the Vas deferens ; posterior end enlarges to form Vesicula seminalis, and extreme end functions as both Vas deferens and ureter.

The histological structure of the kidneys in *Scyllium* is essentially similar to that in the kidneys of *Rana*. They are composed of a mass of urinary tubules, and differentiated into glandular and collecting parts, and possessing Malpighian bodies. The primary uriniferous tubules also open into the dorsal cœlomic space by means of nephrostomes. The tubules are surrounded by a small amount of connective tissue in which run enlarged blood-vessels, the **sinusoids** fed by the renal portal vein and the renal arteries.

CHAPTER X

SCYLLIUM CANICULA—(*continued*)

Nervous System and Sense Organs.

Nervous System and Sense Organs.

Again, as in the frog, we may divide the nervous system and its associated sense organs for convenience in description into Central nervous system, Peripheral nervous system and Sense organs.

The central nervous system, consisting of the brain within the cartilaginous cranium and the spinal cord enclosed in the neural canal, is enclosed in two membranous **meninges,** an outer **dura mater** and an inner **pia mater** as in the frog.

Brain.

The brain does not occupy quite the whole of the space within the cranium, and the interspaces are filled up with a viscid fluid which becomes semi-gelatinous in preserved specimens. Despite the difference in external appearance, owing to the different size and proportion of the parts, the brain in *Scyllium* is composed of essentially the same parts as in *Rana*.

At the front end we find the **telecephalon** or **cerebrum,** which appears as a smooth globular mass at the extreme end of which is a groove. Although it does not appear so from the outside it is, nevertheless, a paired structure, and within it there are two distinct lateral ventricles separated from each other by a median partition of nervous tissue. The two **olfactory lobes,** stout oval masses, are borne, one on each side of the anterior aspect of the telencephalon, on stout stalks, the **olfactory peduncles.** They are closely adherent to the cartilaginous hinder portions of the olfactory capsules through which numerous fibres, collectively constituting the olfactory nerve, pass. The latero-ventral walls of the telencephalon are thickened by masses of nervous tissue corresponding with the **corpora striata** of higher forms, although they are not so well defined.

The cerebrum passes over insensibly into the succeeding narrower part of the brain, namely, the **thalamencephalon,** whose thickened ventro-lateral walls constitute the **optic thalami.** This part is markedly hollow, owing to the presence in it of the enlarged third

ventricle, and it is roofed by a thin membrane. This is composed of a part of the **ependyma,** or epithelium lining the ventricles, and the pia mater. On each side at the front end this dips down into the third ventricle and passes forward into the lateral ventricle, where it becomes highly vascularised and constitutes the choroid plexus of the lateral ventricle. A short distance behind this it again dips inwards in the form of a noticeable transverse fold, the **velum transversum,** which hangs down into the cavity and marks the actual dorsal line of demarcation between telencephalon and

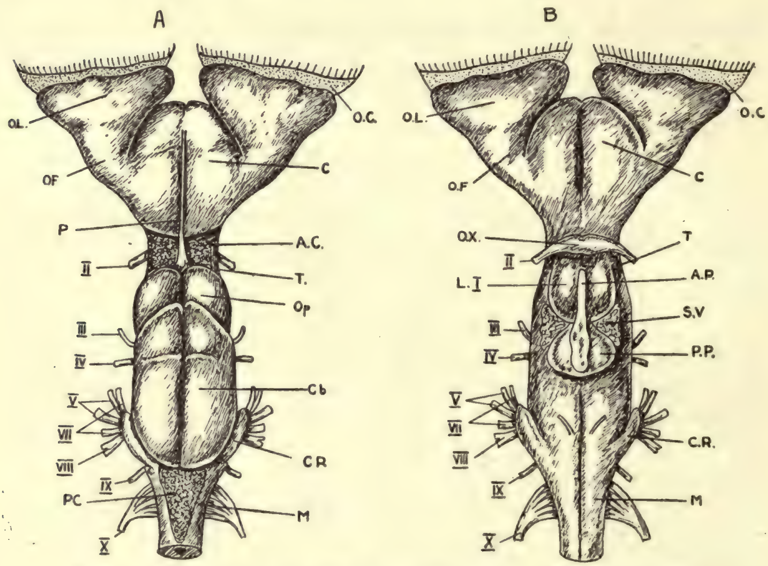


FIG. 82.—Brain of *Scyllium*. A, dorsal view; B, ventral view.

A.C., anterior choroid plexus; A.P., anterior lobe of pituitary body; C., cerebrum; Cb., cerebellum; C.R., restiform bodies; L.I., lobus inferior; M., medulla oblongata; O.C., olfactory capsule; O.F., olfactory peduncle; O.L., olfactory lobe; Op., optic lobe; O.X., optic chiasma; P., pineal stalk; P.C., posterior choroid plexus; P.P., posterior lobe of pituitary body; S.V., saccus vasculosus; T., thalamencephalon; II.–X., cranial nerves.

thalamencephalon. At its posterior end the roof again becomes nervous and bears two ganglionic masses, the **habenular ganglia,** almost meeting in the middle line, but joined by a band of transverse fibres, the **superior commissure.** Just behind this in the middle line arises a small strand which runs forward as the **pineal stalk,** and terminates in swollen enlargement, the **pineal body** or **epiphysis cerebri,** attached to the membrane covering the anterior cranial fontanelle. This is a vestigial structure, being the remnant of a pair of eye-like organs present in ancestral forms. Immediately

behind the point of origin of the pineal stalk is a second transverse band of fibres, the **posterior commissure,** marking the point of juncture of thalamencephalon and mesencephalon.

The anterior end of the third ventricle is limited by the **lamina terminalis,** a strip of nervous tissue on each side of which lies a well-marked opening, the **foramen of Munro,** through which the third ventricle is continuous with the lateral ventricle. The lamina terminalis runs backward, also forming the floor of the anterior part of the ventricle. It terminates at a thick transverse thickening, the **optic chiasma,** which sticks up into the ventricular cavity producing a **pre-optic recess** in front of it, and this marks the ventral boundary between telencephalon and thalamencephalon. The floor of the latter commences with the chiasma, in which the fibres of the optic nerve cross one another, those from the right eye crossing over to the left side of the brain and vice versa. From the sides of the chiasma the two stout optic nerves pass sharply outwards. Just behind this point the floor of the thalamencephalon projects downwards to form a backwardly running lobe, the **infundibulum,** containing a prolongation of the third ventricle. The anterior part of the infundibulum swells out laterally to form two sac-like diverticula, the **lobi inferiores,** whose cavities communicate with that of the infundibulum by oval apertures, while the postero-dorsal portion enlarges to form a wide extremely vascular bag, the **saccus vasculosus.** Closely adherent to the ventral wall of the indundibulum is the **pituitary body** or **hypophysis cerebri.** This consists of an anterior lobe, narrow and stalk-like, attached to the infundibulum between the lobi inferiores, and a much broader posterior lobe which is highly glandular. It is slightly more dorsal than the former, and extends back beyond the saccus.

The **mesencephalon** or **mid-brain,** although small, is easily distinguished. Dorsally it comprises the two **optic lobes** or **corpora bigemina ;** these are small oval swellings separated in the middle line by a furrow and overhung to a large extent by the anterior end of the cerebellum. They are hollow, their cavities, the **optic ventricles,** being offshoots from the brain cavity, and their walls termed the **tectum opticum,** are plentifully supplied with ganglion cells related to the terminations of the fibres from the optic nerves. The sides and floor of the mesencephalon are constituted by nervous masses, the **cruri cerebri,** continuous with the optic thalami in front and the medulla behind. The oculo-motor nerves arise from the ventral surface of the crura. The cavity of the mid-brain is constricted laterally, forming the **Iter** or **Aqueduct of Sylvius.**

The hind-brain in *Scyllium* is large, occupying more than half the entire length of the whole brain. The roof of the front part, or

myelencephalon, is thickened and gives off a large hollow outgrowth, the **cerebellum.** This is an oval structure with pointed ends, and marked by a slight median furrow ; in front it projects freely over the optic lobes and behind over the roof of the fourth ventricle. Its internal **cerebellar ventricle** or **metacœle** opens into the front end of this ventricle. It is connected to the medulla by a solid tract of nervous tissue on each side, the **cerebellar peduncle.** The succeeding part of the brain is the **myelencephalon** or **medulla oblongata,** and, like the thalamencephalon, its roof is composed of ependymal epithelium with which the pia mater is closely associated, and the joint membrane so formed is richly supplied with blood-vessels forming the choroid plexus of the fourth ventricle. The ventral

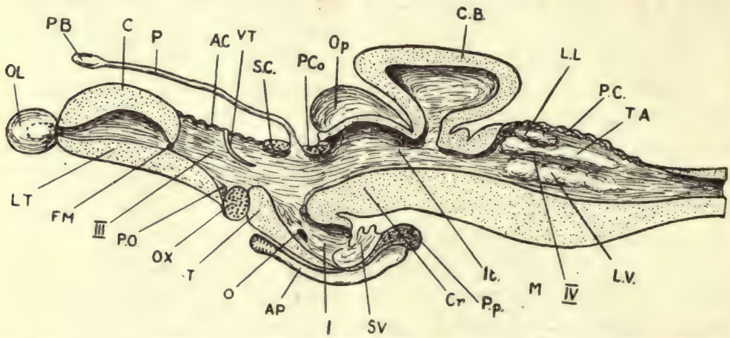


FIG. 83.—Longitudinal section of brain of *Scyllium* slightly out of median plane.

A.C., anterior choroid plexus ; A.P., anterior lobe of pituitary body ; C., cerebrum ; CB., cerebellum ; Cr., crus ; F.M., foramen of Munro ; I., infundibulum ; It., iter ; L.L., lobus lineæ lateralis ; L.T., part of lamina terminalis ; L.V., lobus visceralis ; M., medulla oblongata ; O., opening to cavity of lobus inferior ; O.L., olfactory lobe ; Op., optic lobe ; O.X., optic chiasma ; P., pineal stalk ; P.B., pineal body ; P.C., posterior choroid plexus ; P.Co., posterior commissure ; P.O., pre-optic recess ; P.P., posterior lobe of pineal body ; S.C., superior commissure ; S.V., saccus vasculosus ; T., thalamencephalon ; T.A., tuberculum acusticum ; V.T., velum transversum ; III. and IV., third and fourth ventricles.

and lateral walls of the ventricle are greatly thickened, and contain a large number of ganglion cells which are related to the 5th, 7th, 8th, 9th and 10th cranial nerves. The antero-lateral walls are continued on each side to form the characteristic wing-shaped **corpora restiformia** or **restiform bodies,** passing forward just beneath the hinder end of the cerebellum. In the inside walls of the ventricle are three well-marked projections, the **tuber acusticum,** containing centres related to the auditory fibres ; above it, the **lobus lineæ lateralis,** related to the nerves of the lateral line, and below it the **lobus visceralis.** These two ridges are readily seen if the brain is cut in median longitudinal section. The medulla passes over imperceptibly into the spinal cord.

The cerebrum in *Scyllium,* as in all lower Chordata, is mainly

concerned with the sense of smell, and this is the sense that plays a large part in procuring the fish's food. Thus it is that it is relatively larger than in *Rana*. The cerebellum, on the other hand, is the great centre for the co-ordination of movement, and is also closely related to the lateral line sense organs. Hence, in an active animal like the dogfish, this part of the brain, too, is more developed than in the frog. Tracts of nerve fibres run from the cerebrum to the optic thalami, and thence through the crura cerebri to the cerebellum, medulla and spinal cord, and so we find a system of fibres linking up the various sensory and motor centres of the brain and allowing of a central co-ordination of activities.

Before leaving the brain it may not be out of place to glance briefly at its mode of development, since it is fairly simple in *Scyllium*, and, just as in the adult we have a comparatively simple primitive brain providing a ground plan upon which the brains of the higher Chordata can be built, so we find its development pursues, in general, a course followed, with but slight modification, in other forms. It has previously been pointed out that the whole of the central nervous system arises as a tubular structure by the closure of the medullary folds. From the very beginning the anterior end of the medullary plate, lying in the head region, is wider than in the trunk region, and as the concrescence of the folds is proceeding this region dilates to form at first two and, very shortly after, three distinct sac-like enlargements separated from one another by constrictions. These are the three primary brain vesicles, and are known from before backwards as the **fore-brain** or **prosencephalon,** the **mid-brain** or **mesencephalon** and the **hind-brain** or **rhombencephalon,** the latter passing over gradually into the spinal cord. They lie on the dorsal side of the embryo above the notochord, which terminates abruptly under the mid-brain. The dorsal side of the fore-brain grows much more quickly than the ventral side, with the result that the prosencephalon becomes bent round over the end of the notochord almost at right angles, thus producing what is known as the **cephalic flexure.** This is characteristic of most Craniates, but it disappears again in the dogfish as the adult condition is reached. The folds close slowly towards the front end, so that there is left for some time an anterior opening, the **neuropore,** which, even when it eventually closes, leaves a small depression, the **neuroporic recess.** The end of the fore-brain below the recess is termed the lamina terminalis.

Very shortly after the appearance of the three primary vesicles a hollow outgrowth appears on the lateral wall of each side of the fore-brain towards its ventral margin; this is the **primary optic vesicle.** As development proceeds this differentiates into a distinct

optic vesicle, responsible for the production of the retina, at its outer end, and a tubular portion, the **optic stalk,** connecting it with the brain and marking the position of the future optic nerve. The level where the stalk joins the brain is marked by an **optic groove** running across the floor. This persists in the adult as the pre-optic recess, and it forms an important landmark in the brain, since it marks the hinder end of the lamina terminalis, and also the ventral posterior limit of the telencephalon. The dorsal limit is soon laid down by the appearance of a fold destined to form the velum transversum. The antero-dorsal walls of the telencephalon now grow forward on each side in the neighbourhood of the neuroporic recess, to form the paired cerebral hemispheres, but the brain does not grow actually

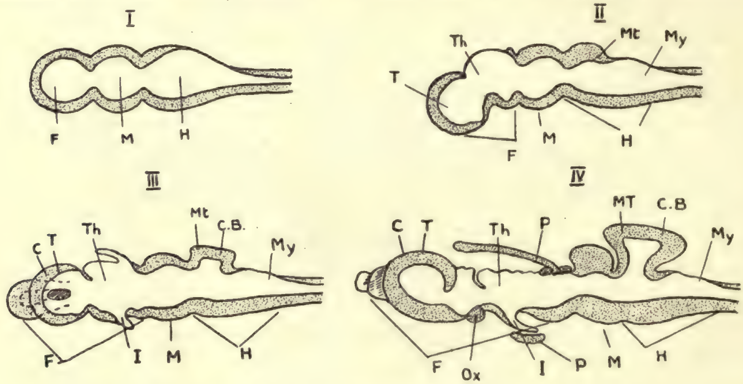


FIG. 84.—Diagram of development of brain of *Scyllium.*

I.–IV., four successive stages in development; II., stage of cranial flexure; IV., late stage, for full naming compare with section of adult brain; C., cerebrum; CB., cerebellum; F., fore-brain, prosencephalon; H., hind-brain, rhombencephalon; I., infundibulum; M., mid-brain, mesencephalon; Mt., metencephalon; My., myelencephalon; OO., optic groove; O.X., optic chiasma; P., pineal outgrowth; Pi., pituitary body; T., telencephalon; Th., thalamencephalon.

in the middle line. Hence even in the higher animals where the cerebral development is great, the lamina terminalis always remains to mark the end of the embryonic fore-brain.

The next part of the brain, the thalamencephalon, is early marked by two median outgrowths, while its roof remains for the most part non-nervous. The dorsal projection is the beginning of the epiphysis cerebri, while the ventral one is the infundibulum. The hypophysis cerebri, however, is not an outgrowth from the brain at all. It arises as a pocket-like diverticulum from the roof of the stomodœum, which then forms a closed vesicle with a solid stalk. The stalk disappears and the vesicle takes up its position beneath the infundibulum.

The roof of the mid-brain vesicle gives rise to two enlargements, the future optic lobes, while its walls and floor become markedly

thickened to form the crura cerebri, and consequently reduce its cavity to a fairly small passage, the iter.

While these processes have been taking place the hind-brain has also been differentiating into its two subdivisions, the metencephalon and the myelencephalon. The roof of the former gives rise to a large median dorsal outgrowth, the cerebellum, while that of the latter remains thin and epidermal. The sides and floor of the whole hind-brain thicken considerably. At the hinder end the myelencephalon thickenings pass over into those of the spinal cord.

The nasal organ and the auditory organ are not derived from the brain like the optic vesicle, but from ingrowths of the ectoderm.

The various parts of the brain in the embryo and the adult and the structures characteristic of each of them may be tabulated in the following manner :—

THE DIVISIONS OF THE BRAIN IN SCYLLIUM CANICULA, AND THE STRUCTURES ASSOCIATED WITH EACH.

Primary and embryonic divisions.	Secondary and adult divisions.	Associated structures.
PROSENCEPHALON or FORE-BRAIN.	TELENCEPHALON.	Rhinencephalon, *i.e.* olfactory lobes. Rhinocœle. Cerebrum (cerebral hemispheres). Lateral ventricles. Foramina of Munro.
		Pre-optic recess; Velum transversum
	DIENCEPHALON or THALAMENCEPHALON.	3rd Ventricle. Anterior choroid plexus. Optic thalami. Habenular ganglia. Superior commissure. Epiphysis cerebri (pineal body). Optic chiasma. Post-optic recess. Infundibulum. Lobi inferiores. Saccus vasculosus. Hypophysis cerebri (pituitary body).
MESENCEPHALON or MID-BRAIN.	MESENCEPHALON.	Posterior commissure. Optic lobes (Tectum opticum). Crura cerebri. Aquæductus Sylvii or Iter.
RHOMBENCEPHALON or HIND-BRAIN.	METENCEPHALON.	Cerebellum. Metacœle.
	MYELENCEPHALON.	4th Ventricle. Posterior choroid plexus. Restiform bodies: Tuber acusticum. Lobus lineæ lateralis. Lobus visceralis. Medulla oblongata.

Spinal Cord.

The spinal cord calls for but brief notice. It is continuous in front with the brain, and thence passes backwards in the neural canal as a cylindrical column, slightly flattened dorso-ventrally and gradually diminishes in size until it terminates at the end of the caudal vertebræ. Above, it bears a shallow **dorsal fissure,** and beneath a deeper **ventral fissure.** In transverse section it exhibits the two characteristic varieties of nervous tissue, an inner mass of grey matter, but not so definitely divided into dorsal and ventral cornua as in *Rana*. Near the middle the **canalis centralis** will be seen as an oval tube lined by a typical epithelium, which is ciliated. Running through both grey and white matter are certain supporting elements termed **neuroglia** cells, which are non-nervous.

Cranial Nerves.

We find in *Scyllium* the same cranial nerves that have already been dealt with in *Rana,* and there is in addition a tiny pair * arising from the front end of the prosencephalon, termed the **nervi terminales**, which are also present, though very small, in the frog. Indeed, the same ten nerves are to be found in all the Craniata, arising from the same place and with the same general distribution, although in higher forms, *e.g.* mammals, there are added to these two more pairs, making twelve in all. The same is probably true of the nervus terminalis, although it is not always so easy to make out as in *Scyllium,* and it is, as yet, not very well known. It is important, therefore, that these nerves and their point of origin should be borne in mind, and for this reason they are set forth in tabular form below.

ORIGIN OF THE CRANIAL NERVES IN SCYLLIUM.

Nervus terminalis.	Arises from the front end of the prosencephalon near middle line.
1. Olfactorius.	Arises in the ectodermal cells of the olfactory organ and passes as a series of small nerves to the olfactory bulb.
2. Opticus.	Arises from the optic chiasma on the floor of the diencephalon.
3. Oculomotorius.	Arises from the ventral surface of the crura cerebri, mescencephalon.
4. Patheticus.	Arises from the *dorsal* side of the metencephalon, in the angle between the optic lobes and the cerebellum.

* There is also a small nervus septalis arising behind the olfactorius, but it is omitted here on account of its small size.

5. Trigeminal.	Arises from the latero-ventral aspect of the myelencephalon below restiform bodies, by two roots; a large dorsal sensory root bearing the Gasserian ganglion and a smaller ventral motor root.
6. Abducens.	Arises from the median ventral aspect of the myelencephalon.
7. Facialis.	Arises by two main roots, sensory and motor, which unite to form the geniculate ganglion, from the lateral aspect of the myelencephalon.
8. Auditorius.	Arises directly behind 7.
9. Glosso-pharyngeal.	Arises by two or three roots from the latero-ventral aspect of the myelencephalon behind and below 8.
10. Vagus.	Arises by four main roots from the lateral aspect of the myelencephalon. The most anterior, which is that of the lateral line nerve, is just behind and dorsal to 9.

The foramina through which these nerves leave the cranium have already been dealt with, so that the next point is to consider their distribution. The first, or **olfactory nerve,** passes through the posterior wall of the olfactory capsule as a series of fibres which are distributed to the olfactory epithelium. The second, or **opticus,** passes through the side wall of the orbit, up to the optic stalk, and is distributed to the retina. The third, or **oculomotorius,** also perforates the orbital wall and supplies the superior, internal and inferior oblique muscles of the eyeball. The fourth, or **patheticus,** enervates the superior oblique eye muscle. The fifth, or **trigeminus,** after leaving the ganglion, divides into two branches inside the cranium, of which the anterior, a sensory branch, passes out into the orbit as the **ophthalmic** branch of the fifth nerve. This runs forward along the mesial dorsal wall of the orbit and out through its roof to the skin of the dorsal side of the front end of the head and snout. The posterior branch enters the orbit by a common foramen with the sixth and part of the seventh nerves, and quickly divides into two, the **maxillary** and **mandibular** nerves. They pass antero-laterally across the floor of the orbit, and the former goes to the skin and muscles of the upper jaw and lip, while the latter spreads out in the skin and muscles of the lower jaw. The sixth nerve, or **abducens,** goes to the external rectus muscle.

So far the distribution of the cranial nerves has been typical, but when we come to the seventh, or **facial nerve,** we find a striking difference between *Scyllium* and *Rana*. In the first place it is really a mixture consisting of the branches of the facialis proper, such as we find in all Craniates and another series of fibres belonging to the

system of the lateral line sense organs, and so termed lateralis fibres. Such lateralis nerves are found generally in fishes, and in those members of the class Amphibia that permanently inhabit the water, but are absent from all the air-breathing vertebrates. The anterior or **ophthalmic branch** of the seventh is a lateralis nerve, and runs into the orbit, where it accompanies the ophthalmic branch of the trigeminus forward to the snout. There it serves the sensory ampullæ and canals of the supra-orbital and snout regions It even arises by a separate root from the brain. The second branch of the seventh, the **buccal,** is also composed of lateralis fibres, and passes in company with the maxillary and mandibular branches of the fifth

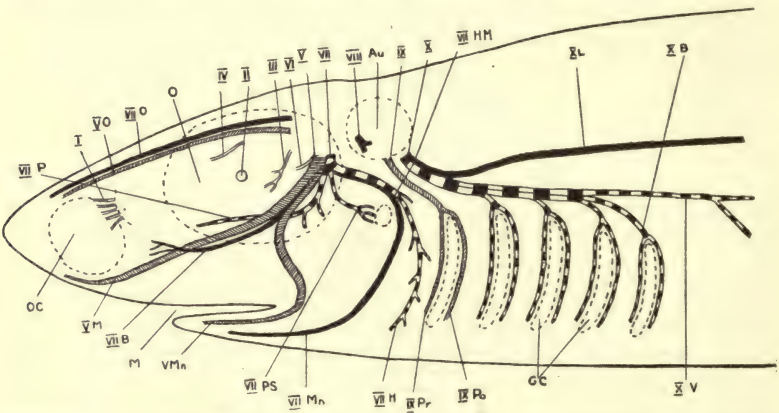


FIG. 85.—Diagram of distribution of cranial nerves in *Scyllium*. The factors of the acustico-lateralis system shown in black.

Au., auditory capsule; G.C., gill cleft; M., mouth; O., orbit; O.C., olfactory capsule. I.–X., cranial nerves; V.M., maxillary; V.Mn., mandibular; V.O., ophthalmic; VII.B., buccal; VII.H., hyoidean; VII.Hm., hyomandibular; VII.Mn., external mandibular; VII.O., ophthalmic; VII.P., palatine; VII.Ps., prespiracular; IX.Po., post-trematic branch; IX.Pr., pre-trematic branch; X.B., branchial dividing into pre- and post-trematic branches; X.L., nervus lineæ lateralis; X.V., visceral.

nerve to the sensory canals in the infra-orbital region and on the ventral surface of the snout. Immediately on entering the orbit, the **palatine** or first branch of the facialis proper passes forwards and outwards, at first behind and then below the maxillo-mandibular of five to the lower jaw. Here it divides into two, one penetrating the jaw and the other passing to the muscles of the roof of the buccal cavity. The fourth and largest trunk of the seventh nerve runs along the hinder wall of the orbit, giving off several pre-spiracular twigs which supply the anterior wall of the spiracle, and then crosses the hyomandibular cartilage, just beneath the skin, to the posterior wall of the spiracle. It separates into three main portions; two post-spiracular twigs consisting of true facialis fibres, supplying the

mucous membrane and muscles of the hyoid arch, and the third, a lateralis nerve, distributed as the **external mandibular** to the sensory canals and ampullæ in the hyoid and mandibular regions.

The eighth nerve, the **auditory,** passes directly to the membranous labyrinth of the ear, over which it spreads. The ninth, or **glosso-pharyngeal,** nerve leaves the cranium by an aperture in the post-orbital groove, and has three main branches. The first is a small dorsal factor to the skin ; the second is a palatine branch running forward to join with the similar branch from the facial. The third and largest branch soon divides into two, one passing in front of, and the other behind, the first gill cleft to the structures surrounding which they are related.

The tenth or **vagus nerve,** like the seventh, contains also an admixture of lateralis fibres. In the same way, too, the lateralis nerve, a large branch, arises from the medulla by its own root, and, although joining the main trunk for a short distance, soon leaves it again to pass backwards fairly superficially in the myoseptum between the epiaxial and hypaxial portions of the myomeres just under the lateral line canal whose sense organs it supplies. The second branch of the tenth is the **visceralis** nerve, consisting of true vagus fibres, passes back to the heart and other viscera. The third branch sends a factor to each of the four posterior gill clefts, over which they split into a pre- and a post-branchial portion. This third branch also is not found typically developed in air-breathing vertebrates where, of course, the gills are absent, but is probably represented in them by the pulmonary branch of the vagus.

When we consider the functions of the cranial nerves we see that they can be divided into three groups. The first is composed of the oculomotorius, the patheticus and the abducens, all of which are entirely motor in function, and as they go solely to muscles, in this case eye muscles, they are termed **myomeric nerves.** The second group, consisting of the olfactorius, the opticus, the auditorius, the lateralis nerves and, perhaps, also the nervus terminalis, is solely concerned with conveying impressions to the brain, and hence its constituents are termed sensory nerves. The remainder of the cranial nerves are both sensory and motor in function, and so spoken of as **Mixed nerves ;** viz. the trigeminus (of which, however, the ophthalmic branch is entirely sensory), the glosso-pharyngeus and the branches of both the facialis and the vagus that are not lateralis nerves.

All the lateralis nerves, namely, the ophthalmic, the buccal and the external mandibular of the facialis, and the lateral line nerve of the vagus, in spite of the way in which they leave the cranium, all originate in the lobus lineæ laterals in the medulla. This large nerve

centre is closely bound up with the tuber acusticum, from which the eighth nerve arises. Furthermore, other reasons lead us to regard the ear as a specialised portion of the lateral line series of sense organs, and so we sometimes speak of these two large brain ganglia and all the nerves directly related to them as the **acustico lateralis system**. Of this entire complex only the auditory centre and nerve are present in the higher Craniata, *i.e.* many of the Amphibia, all the Reptiles, the Birds and the Mammals.

The manner in which the mixed nerves are distributed also calls for notice. It will be seen that they have a very similar arrangement. Each consists, when reduced to its simplest expression, of three principal parts. One going to the front of a gill cleft, and so termed the pre-branchial or **pre-trematic** branch, well shown in the seventh, ninth and tenth nerves. Another, the post-branchial, or **post-trematic** branch, lies behind the same gill slit. The third branch is situated more dorsally and passes forward, *e.g.* the palatines of the seventh and ninth. It is clear, then, that the trigeminus is related to the mouth in the same way that the others are to the gill clefts, so that for this and other reasons the mouth is regarded by some authorities as representing the fusion of an anterior pair of gill slits. In order to indicate this characteristic method of distribution of the mixed nerves they are sometimes spoken of as **branchiomeric nerves.**

Spinal Nerves.

The spinal nerves only call for brief notice. The typical nerve arises from the cord by two roots, a dorsal and a ventral, of which the former bears a ganglion and arises slightly behind the latter. A pair of such nerves is present in each somite of the body. The five anterior spinal nerves, together with three small so-called spino-occipital nerves that come off by single roots from the hinder end of the medulla in line with the ventral roots, join to form one trunk. The nerve so constituted is distributed partly to the ventral surface of the pectoral fin and partly to the sub-pharyngeal musculature. Spinal nerves 6–11 approximate closely to one another to form a very rudimentary sort of brachial plexus, and then pass on to supply the pectoral fin.

Sympathetic Nerves.

These are quite inconspicuous in *Scyllium*, but consist of two longitudinal chains bearing very small ganglia and lying on the dorsal wall of the abdominal cavity, one on each side of the vertebral column.

Sense Organs.

In addition to the sense organs dealt with in the frog, and which will be referred to again briefly here, namely, the olfactory, the gustatory, the tactile, the optic and the auditory, the dogfish possesses also a series of cutaneous sense organs. These are widely distributed over the body, and are characteristic of fish in general. Of such organs two distinct varieties are present, those termed the **taste buds** or **end buds,** and the sensory organs of the lateral line, the **neuromasts.**

The end buds are very similar to the taste corpuscles of the higher Craniates. They consist of a number of long rod-like sense cells aggregated together in a characteristic manner about a central cell, each possessing a hair-like process projecting above the general level of the epidermis. Closely connected with their deeper ends are arborisations of sensory nerve fibres coming entirely from the facial, glosso-pharyngeal and vagus nerves. In the air-breathing Craniates such organs are confined to the buccal cavity, whereas in the dogfish they are spread irregularly over the surface of the head and branchial region, and in the case of some bony fishes they are even to be found on the body and at the bases of the fins. They not only subserve the function of taste, as we understand it in the higher animals, but, when situated outside the buccal cavity, also inform their possessor when its proper food is near at hand.

The neuromasts are composed of fewer sensory cells, but each individual cell is larger and somewhat pear-shaped. As in the end buds, the cells have a hair-like sensory process. These organs are supplied exclusively by fibres from the lateralis nerves, and are always situated below the external surface of the body and covered by a fluid or semi-gelatinous substance in which their processes lie. The ampullæ are arranged in definite groups on the head and consist of fairly deep tubes swelling out into a chamber at their inner end in which the sensory cells are situated. The lateral line organs are to be found in a series of canals of which the most conspicuous is the lateral line itself. In addition to this, which as noted previously, runs from just behind the spiracle right down the tail, there are also a canal above the eye, the **supra-orbital,** one below the eye, the **infra-orbital,** one in the hinder dorsal part of the head, the **occipital,** and one in the neighbourhood of the hyoid arch and lower jaw, the **hyomandibular canal.**

Eye.

The eye in *Scyllium* calls only for brief notice, since it is in the main similar to that of the frog, the differences being in detail

only, and the same is true, too, of its histological structure. The eyeball itself is almost hemispherical, as it is much less curved on its external side than in vertebrates generally, and the cornea itself is practically flat instead of being curved. The lens is approximately spherical and not bi-convex as in the frog. This fact in conjunction with the flattened cornea causes the anterior chamber to be relatively small, and such a combination of characters is found generally in fishes. Lastly, between the pigment layer of the retina and the choroid coat there is present in the dogfish a peculiar membranous layer which, over the posterior region of the eyeball, possesses a curious bright, silvery metallic lustre. It is known as the **tapetum,** and presumably causes the reflection of a certain amount of light. Vision in the dogfish is apparently much less keen than in higher animals.

Ear.

In *Scyllium* and fish in general the ear is less complex than in the land-dwelling vertebrates, and it consists only of the membranous labyrinth or internal ear, and we find nothing to correspond with the middle ear, *i.e.* the tympanic membrane and cavity as it exists in *Rana*. On account of its larger size and greater accessibility the labyrinth is more easily studied in the dogfish than in the frog. It lies embedded in the cartilaginous olfactory capsule on the outer walls of which, as we have already noted, are three ridges marking the position of the canals within. The vestibule is a very thin-walled laterally compressed sac, distinctly marked off into two portions ; the upper, or utriculus, is elongated and triangular in shape, the lower, or sacculus, is a smaller more rounded sac in open communication with it. The semicircular canals bearing ampullæ, and coming off from the utriculus are well developed and present certain peculiarities. The anterior and posterior canals

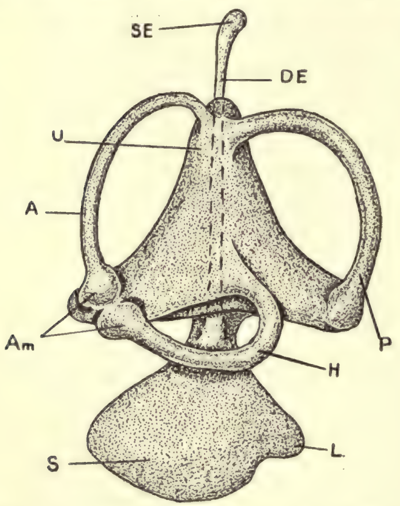


FIG. 86.—Diagram of ear of primitive Craniate, adapted from Wiedersheim.

A., anterior vertical semicircular canal; Am., ampulla; D.E., ductus endolymphaticus; H., horizontal semicircular canal; L., lagena; P., posterior vertical semicircular canal; S., sacculus; S E., saccus endolymphaticus; U., utriculus.

join up on the dorsal side, and open by a common aperture, while the posterior canal takes the form of an almost complete ring communicating with the utriculus by a single opening. The ductus endolymphaticus, coming off from the sacculus, runs dorso-mesially to open on the dorsal surface of the skull by an aperture situated in a depression at its hinder end. When treating of the cranial nerves we saw that the enervation of the ear and lateralis system was closely connected. Furthermore, the actual structure of the sensory cells in the ear is practically identical with those of the neuromasts, and they function in the same way, for in each the actual receptive process is surrounded by liquid, the vibrations of which bring about its stimulation. Lastly, when we come to study the development of the embryo, it is found that the ear and the lateral line system all start from a peculiarly modified patch of thickened ectoderm in the hind brain region, so that we consider the ear as simply a highly-specialised portion of the lateralis system.

This, then, completes our survey of the dogfish, a simple vertebrate animal eminently adapted for life in the water, and one that exhibits, in spite of certain modifications, the main plan of a Chordate in a little specialised form. It is further of interest, since the anatomical relations of certain of its organs, blood-vessels, etc., are closely approached in the developing embryo of the higher animals, including man himself.

CHAPTER XI

LEPUS CUNICULUS

A Mammal—*Lepus cuniculus*, the Rabbit—Introduction—External characters —Skin—Muscular System—Skeleton and the Skull of the Dog.

A Mammal—*Lepus cuniculus*, the Rabbit.

The Class Mammalia includes the highest animals alive in the world and reaches its culmination in man himself who, while not so highly specialised structurally as some other forms, is nevertheless characterised by such a high degree of mental development that he must be regarded as the dominant form in the class. Mammals are cœlomate, chordate, craniate animals and so possess all the general characters implied by those terms. In certain points they resemble the frog much more closely than the dogfish. Thus, for example, they possess an endoskeleton composed mainly of bone and modified pentadactyl limbs. The pericardium lies within the cœlom, respiration in the adult takes place by means of lungs and not gills and the air passage opens within the buccal cavity by a pair of internal nares. Lastly the urinary bladder is not an enlargement of the kidney duct, but an outgrowth of the cloaca of the embryo.

The differences from both the dogfish and the frog are numerous and important, and practically constitute the diagnostic characters of the class. It is only necessary to call attention to the main ones here, since the detailed differences will appear in the course of an examination of a particular example. A well-marked exoskeleton is present in the form of hairs, each springing from an encasing sheath or follicle, constituting in most species a more or less complete covering for the body and also as claws, nails or hoofs occurring at the ends of the digits. The skin also bears two kinds of glands, distinguished as sweat glands and sebaceous glands, both arising in connection with the hair follicles. Certain of the sweat glands on the ventral surface are modified to form the **mammary** or **milk glands,** from the presence of which the class receives its name. In all save the lowest members of the class (*Ornithorhynchus* and *Echidna*) the mammary glands open in groups on projections of

the body wall termed the **mammæ** or **teats**, and these structures with their associated glands are much better developed in the female than in the male. Well marked external ears or **pinnæ** are also present, and typically they are capable of being moved by a special set of muscles. In the adult of higher mammals there is no cloaca, so that the anus opens quite separately from the urogenital aperture in both sexes. Both openings lie on a characteristic area known as the **perineum** on the posterior ventral abdominal wall in the region of the hinder end of the pelvic girdle, and with this certain **perineal glands** are associated. A notochord is of course present in the embryo, but with the complete ossification of the vertebræ in the adult it disappears save for a small remnant in the middle of the centra of certain species. The vertebral column consists of a moderate number of vertebræ which are differentiated into five regions, the cervical, the thoracic, the lumbar, the sacral and the caudal. The first cervical vertebra, termed the **atlas**, is modified for articulation with the skull, while the second, the **axis** or **epistropheus**, forms a very striking joint with the atlas by means of which the rotation of the skull can be brought about. The skull itself is a far more solid and compact structure than we have previously encountered and has the orbit sunk deeply in it, so that this cavity becomes largely or completely surrounded by bones on the internal side. The suspensory apparatus of the lower jaw is completely incorporated with the cranium, so that the jaw actually articulates with that structure, a type of suspension that is termed **autostylic.** In the frog the internal nares open into the front end of the buccal cavity, but in the mammal, owing to the formation of a sort of false roof to the mouth, the **palate**, partly consisting of bone, the **hard palate**, and partly of mucous membrane, the **soft palate**, the internal nares come to open far back at the begining of the pharynx. No columella auris is present, but its place is taken by a very characteristic chain of tiny bones, the **auditory ossicles.** During the life of the animal two distinct sets of teeth make their appearance in the jaws ; the first occurring in the young animal being termed the **milk teeth**, and these are later replaced by the so-called **permanent teeth** of the adult. This condition is termed **diphyodont**, to distinguish it from that in the dogfish, where there are many successions of teeth. Not only this, but we also find that the teeth are **heterodont**, that is to say, may be differentiated into different types to subserve special functions, and in a typical mammal we can recognise **incisors**, **canines**, **premolars** and **molars.** A series of thin curved movable bony rods, the **ribs**, are developed and they articulate on the dorsal side with the vertebræ and on the ventral side with the sternum. These afford protection to the heart and lungs, and as the hind limbs are more

important in locomotion we find the pectoral girdle is poorly developed. On the other hand, owing to the greater use of the hind limbs, the pelvis girdle is large and securely attached to the backbone.

The cœlom is completely divided into two cavities, by the development of a partly membranous, largely muscular arched partition, the **diaphragm,** situated in the region of the hinder end of the ribs. Thus we can recognise an anterior, **pleural cavity,** lying in a part of the body termed the **thorax,** containing the lungs and having within it the pericardial cavity and a posterior one, situated in the **abdomen,** termed the **peritoneal cavity,** which contains the rest of the viscera. The movements of breathing differ completely from those in *Rana.* Air is drawn into the lungs by the enlargement of the thorax either by the movement of the ribs or the flattening of the arch of the diaphragm, or more commonly both combined.

The kidneys are **metanephroi** and the ureters open directly into the bladder, not serving for the passage of the sperms during any part of their course. In the female, the lower ends of the oviducts are modified to form characteristic structures, the **uteri,** which in some cases fuse together forming a single **uterus.** The ova (save in *Ornithorhynchus* and *Echidna*) are minute and practically yolkless, although their structure and mode of development give distinct indications that they have been derived from eggs with a large amount of yolk such as we find in reptiles. Save in the forms just mentioned the eggs are never passed to the outside, but undergo development within the uterus to the walls of which they are attached for a short time (Marsupials) or a relatively long time (as in higher mammals, Eutheria) by a very characteristic organ termed the **placenta.** This is composed of an intimate union of tissues from both mother and embryo and serves for the transference of food, oxygen, and excretory products. After birth the young animals are quite incapable of obtaining food for themselves and are dependent upon the milk secreted by the mammary glands of the mother.

The heart of the mammal is completely divided into two sides by the **interatrial septum** and the further development of a median partition, the **septum ventriculorum,** in the ventricle, and the two sides have no means of intercommunication. More than that, in order that the blood in a ventricle may return to it again, it is necessary for it to leave the heart twice, once to go to the tissues and return and once to go to the lungs and back. We refer to this condition as a **complete double circulation.** The heart contains only four chambers, two auricles, or better atria, and two ventricles, there being no distinct sinus venosus and no conus arteriosus. A hepatic

portal system is present as in all Craniates, but a renal portal system is absent. The mammals are warm blooded, that is to say, the blood is maintained at a fairly constant temperature somewhere just below 100° Fahr., and this is quite independent of the variations of the temperature of the surroundings.

The brain is extremely well developed in the mammals, particularly in the cerebral hemisphere which in some animals, for example man, forms the largest part of the brain. Their surfaces are thrown into a series of folds or **gyri**, separated from one another by well-defined grooves or **sulci,** whereby the amount of space at the periphery of the hemispheres, in which the nerve cells lie, is greatly increased. The main part of this increase is due to the formation of a new portion of the roof of the cerebrum termed the **neo-pallium,** which is not found in the lower animals. The optic lobe on each side is divided so that there are two pairs of bodies, the **corpora quadrigemina.** The sense organs are also strongly developed, and in the internal ear we find a spirally coiled structure, the **cochlea.**

With this short discussion of the general characters of the class, we can pass on to consider a particular example in the rabbit. *Lepus cuniculus*, the ordinary wild rabbit, belongs to the genus *Lepus,* which includes among other forms *L. timidus* the hare, and *L. variabilis,* the Arctic hare or Snowshoe rabbit. It is a very common animal in practically all parts of the British Isles, and is the species most widely kept in captivity when, as is well known, it exhibits a wide range of variation in colour, general size and build, and so on. This phenomenon of variation under domestication is a common one, and is marked in cats, dogs, cattle, pigeons, fowls, etc., to a greater or less extent when they are domesticated by man. Years ago the rabbit was introduced into Australia, where, free from the enemies and other checks that keep its numbers down in its native lands, it has multiplied to such an extent that it has become a serious menace to the farmers. This is an illustration of what may happen when the equilibrium in the animal life of a given area that is established in the course of a long period of time, is upset by man introducing a new animal.

External Features.

Externally we can readily distinguish in the body of the rabbit a head, a neck, a trunk, a tail and two pairs of limbs, all of which are covered with a dense growth of fine hair, the fur. The manus possesses five digits, while the pes has only four. The colour in the wild form is a dark brownish-grey above, shading off to a lighter grey on the sides, and becoming practically white underneath.

The underside of the tail and adjacent perineal regions of the body are quite white. Altogether it is very inconspicuous against almost any background in the light of the early morning or evening, when it comes out to feed. It passes most of its time in a burrow in the ground, and a number live close together, each pair with their own hole, forming a community termed a warren.

The front end of the head is drawn out into a blunt snout. The mouth is not large, but noteworthy in that the upper lip is cleft vertically in the middle line, a feature that enables the animal to employ its teeth for gnawing without this lip getting in the way. Above the mouth are the openings of the two external nares. The upper lips bear a series of long stout hairs, the **vibrissæ,** whose roots have the endings of certain nerves specially related to them, and so constitute a sensory apparatus of considerable use to the animal for feeling its way in its dark underground home. The eyes are large, but not prominent, and provided with well-developed upper and lower lids. At their inner corner, or **canthus,** is the nictitating membrane, which is capable of being drawn partly across the eye. External ears, or pinnæ, are strongly marked and well provided with muscles ; in some domestic varieties they do not stand upright as in the wild form, but droop down over the sides of the head, producing a variety known as a lop-eared rabbit.

The perineum is marked by bearing white fur. On it open the alimentary canal by the anus and the urogenital ducts, and it also has a pair of small **perineal pouches** and two small bare areas on which open the ducts of the **perineal glands** to the secretion of which the animal owes its characteristic odour. The rabbit, like all mammals, is diœcious, and so the perineal areas of the two sexes are different. The female urogenital aperture is a slit-like opening, the **vulva,** bearing in its roof at the ventral end a rod-like structure, the **clitoris.** The corresponding aperture in the male is borne at the end of a conical rod-like projection, the **penis,** which is covered by a fold of skin, the **prepuce**, so that at first sight the urogenital apertures of the two sexes appear somewhat similar. On the perineum of the male at each side of the base of the penis lies a small **scrotal sac,** within which is contained the **testis.** It is characteristic of most mammals that the testes leave their primitive position on the dorsal side of the abdominal cavity, and pass into a single or paired outgrowth of the peritoneal cavity which projects on the outside of the body in the perineal region. The last of the external features that call for notice are the mammary glands. These number four or five pairs, situated on the lines joining the armpits, or axillæ, and the corresponding or inguinal regions of the leg. In the male, although present, they are hard to distinguish ; in the female,

however, they are more marked and become large after the birth of the young. They are marked externally by papilla-like projections known as the teats or **mammæ.** The ducts of the gland open on to the apex of this projection, and so form an outlet through which the young animal can suck the milk that is its only food for the first weeks of its life.

Integument and Muscular System.

The skin of the rabbit fits far more closely to the underlying muscular tissue than in the frog, for there are no subcutaneous lymph sinuses. A certain amount of independent movement is provided for, however, by the development of a layer of **subcutaneous** or **areolar connective tissue,** which connects the skin to the body wall. The structure of this tissue has already been dealt with. The detailed structure of the skin and its glands also differ in *Rana* and *Lepus*, although both are composed of the same two fundamental layers, the epidermis and the dermis.

The epidermis is a stratified epithelium divisible into two layers ; it is derived from the ectoderm of the embryo, and to be regarded as forming a protective layer for the underlying tissues. Its basal portion is composed of a number of layers of polygonal cells, which are composed of protoplasm and contain nuclei. These constitute the **rete mucosum** or **Malpighian Layer,** and the cells at its outer side become filled with secretory granules. The outer layer of the epidermis, known as the **stratum corneum,** is many layers thick, and the cells become more and more flattened as they pass outwards, at the same time their nuclei disappear and the protoplasm becomes replaced by a substance allied to keratin, a process termed cornification. The outermost cells form small dead horny scales that are constantly being shed. As noted above, this is a protective layer, and in certain parts, for example the heel of man, becomes extremely thick.

The **dermis** or **corium** is composed of dense connective tissue, which on its outer side is thrown up into a series of folds into which pass the blood vessels nourishing the skin, and in which are situated the various touch corpuscles. As it passes inwards the texture of the dermis becomes looser, and it incloses islets of fatty tissue, and finally it merges into the subcutaneous tissue.

Hairs, the characteristic covering of the mammalian skin, are the products of the epidermis, and are borne in deep tubular pit-like downgrowths of that layer termed the **hair follicles.** Each hair is a long rod-like structure with an enlarged root, and contains an axis or medulla of large angular cells containing granules and sometimes air globules. Surrounding this is a fibrous layer composed of long

fibrillated cells, which in dark-coloured hair contain numerous granules of a dense pigment. The outside is covered by a layer of thin imbricated scales, the **hair cuticle.** At the bottom of the follicle the hair expands to form a bulbous root, which is the actual growing point and composed of soft protoplasmic cells. Into this root fits a projection of the cutis termed the **hair papilla,** which is plentifully supplied with blood-vessels. Often when the hair is pulled out the epidemal portion of the follicle comes with it so that it is sometimes termed the root sheath. Where the epidermis is

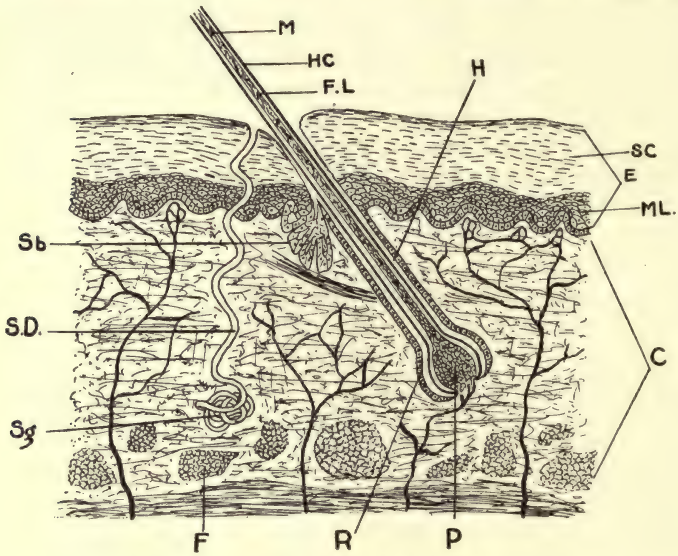


FIG. 87.—Diagram of section of skin of mammal.

C., corium or dermis ; E., epidermis ; F., fat ; F.L., fibrous layer ; H., hair follicle ; H.C., hair cuticle ; M., medulla ; M.L., Malpighian layer ; P., hair papilla ; R., root sheath ; Sb., sebaceous gland ; S.C., stratum corneum ; S.D., duct of sweat gland ; Sg., sweat gland.

turned in to form the follicle it is composed of two layers as on the skin itself : the outer one corresponds with the stratum corneum, and therefore comes to lie next to the hair itself, and is termed the **inner root sheath,** being in itself composed of three layers of cells ; the **outer root sheath** corresponds with the rete mucosum, and is considerably thicker at the upper end, but thins off towards the base. Outside these epidermal layers the cutis furnishes a **hyaline layer** in the form of a fairly thick basement membrane, and around this again, a layer composed of flattened fibres and cells circularly arranged. The nerves of the corium penetrate the hyaline membrane and arborise on the outside of the outer root sheath. In the vibrissæ

they are particularly well developed and exhibit a characteristic structure: such sensory hairs also possess a series of venous sinuses at their bases.

Primitively connected with the hair follicle of the mammal are two sets of glands, the sweat and the sebaceous glands. The latter are small saccular glands lined by a secretory epithelium composed of characteristic large cells. They arise singly or in pairs about half-way down the follicle. The cells secrete a fatty substance and then themselves disintegrate in order to produce the characteristic sebaceous secretion. The sweat glands are developed from higher up the follicle, and may later lose connection with it altogether. When fully formed, they consist of a long corkscrew-like duct passing deep down into the dermis to terminate in a fairly closely coiled secretory tubule. The secretory portion is lined by a cubical epithelium, and the sweat is produced in the cells and passed out into the lumen. In man these glands are developed all over the general surface of the body, and are particularly numerous on the palms of the hand, but in the rabbit they are restricted to certain limited areas.

The mammary glands are highly modified sweat glands producing their secretion, the milk, in a similar manner, and they are developed in connection with special groups of hairs along the axillary-inguinal line.

The muscular system of the rabbit calls for little special notice, since it is not intended to enter into a detailed description of the individual muscles. It is divisible, as in the frog, into voluntary or striate muscles and involuntary or non-striate muscles, and also the heart is composed of characteristic cardiac muscle. The whole of the ventral and lateral regions of the trunk and the neck have a thin layer of **cutaneous muscle** attached closely to the inner side of the skin, and so enabling the animal to twitch its skin quite independently of the underlying body wall. Recti Abdomnis and oblique muscles essentially similar to those in *Rana* are found in the abdominal region ; but inside the oblique is a further thin muscular layer, the **transversalis** covered by the peritoneum. In the thoracic region, however, this arrangement is broken up by the ribs, and we find it replaced by a series of **internal** and **external intercostal** muscles which play an important part in respiration. Yet one further structure deserves attention, and that is the **diaphragm.** This is a thin arched sheet with a tendinous centre into which are inserted radial muscles originating in the ribs and on the vertebral column, and it completely separates thoracic and abdominal cavities. Two particularly strong bands known as the pillars of the diaphragm pass dorsally one to each side of the vertebral

column. Contraction of the muscles flattens the curvature of the diaphragm and so enlarges the thoracic cavity, a considerable factor in breathing.

Skeleton.

The skeleton in the very young mammal is entirely cartilaginous, but in the adult comes to consist almost exclusively of bone which may be cartilage bone replacing the cartilage or membrane bone developed in the membranes around the cartilage. In addition to this we find in the mammals a third variety, the **sesamoid bones,** which are bony nodules developed in certain tendons where they pass over a joint, and they serve to alter the direction of pull. The skeleton as a whole is composed of the same general factors as in *Rana*, and like it is divisible into an Axial portion composed of the vertebral column and skull and an appendicular portion comprising the limbs and girdles.

The vertebral column consists of a long chain of bones about forty-five in number, and falls into five definite regions, each distinguished by certain characteristic features : these are, the cervical with seven vertebræ, the thoracic with twelve or thirteen, the lumbar with six or seven, the sacral with three or four, and the caudal with fifteen or sixteen. A typical vertebra consists of a centrum, neural arch and transverse and other processes. The centrum is a short bony rod that ossifies from three centres, and so possesses well-marked epiphyses which do not become firmly fused until the animal is quite old. The articulating surfaces of the centra are not separated by synovial cavities as in the frog, but by fibro-cartilaginous **intervertebral discs,** and in the sacral region the centra are actually fused together. The neural arch consists on each side of a **dorsal lamina** meeting its fellow in the middle line at the **neural spine** and joined to the centrum by a narrow portion, the **pedicle,** so leaving at the front and hinder end an **intervertebral notch**, which with the similar notch on the adjoining vertebra leaves an **intervertebral foramen** through which the spinal nerves leave the neural canal. Pre- and postzygapophyses are present on all the vertebræ save the first two, and a number of the caudals and transverse processes on all save the posterior caudals.

The atlas or first vertebra differs markedly from all the others, it is marked by the presence of a large neural canal divided in life by a stout transverse ligament (which may persist in the dried skeleton in a shrivelled condition or be lost) into a dorsal portion, the neural canal proper and a smaller ventral portion which occupies much of the space usually taken up by the centrum, that body being much reduced in size. The neural spine is also reduced, being

simply a low ridge most marked anteriorly. At the front end are two large articular facets for articulation with the occipital condyles of the skull. The transverse process is a wide flat lamina grooved on its posterior edge for the second spinal nerve. The rib is represented by a flat plate of bone joining the transverse process and leaving a triangular aperture for the passage of the vertebral artery.

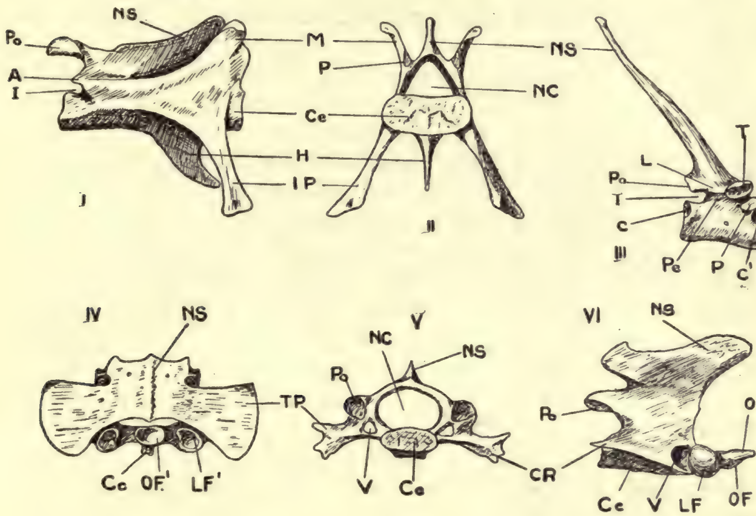


FIG. 88.—Vertebræ of *Lepus*.

I., Lumbar vertebra, side view; II., lumbar vertebra, front end; III., thoracic vertebra, side view; IV., atlas, dorsal view, slightly reduced; V., cervical vertebra, posterior end; VI., axis or epistropheus, side view.

A., anapophysis; C., C′., facets for articulation with capitulum of rib; Ce., centrum; C.R., cervical rib; H., hypapophysis; I., intervertebral notch; L., lamina; L.F., lateral surface for articulation with atlas; L.F′., facet for articulation with lateral surface of axis; M., metapophysis; N.C., neural canal; N.S., neural spine; O., odontoid process; O.F., articular surface on odontoid process; O.F′., articular facet for articulation with odontoid process; P., prezygapophysis; Pe., pedicle; P.O., postzygapophysis; T., facet for articulation with tuberculum of rib T.P., transverse process; V., vertebrarterial canal.

This aperture, the **vertebrarterial canal,** passes upwards through a foramen in the neural canal through which the artery enters and the first spinal nerve leaves the canal.

The second vertebra, the axis or **epistropheus,** has a broad flat centrum produced anteriorly into a peg-like **odontoid process,** which is really the main part of the centrum of the atlas that fuses with the centrum of the axis during development. The neural spine forms a large vertical spine that projects forward some way over the atlas. The anterior end of the centrum bears two facets for articulation, with corresponding surfaces in the first vertebra, and the posterior end bears zygapophyses that are quite typical and have their facets

facing outwards and downwards. The transverse process is short, but stout, being in reality a portion of a rib fused with a true transverse process and the combined structure is perforated by a vertebrarterial canal through which the vertebral artery runs.

The remaining cervicals are characterised by a small flattened centra, only moderately developed neural spines and stout transverse processes formed by the fusion of part of a rib with the transverse process, and this combined structure is pierced by the vertebrarterial canal.

The thoracic vertebræ are readily distinguished by bearing movably articulating ribs. Their neural spines are very strongly developed, forming long stout flattened rods, of which the tenth is approximately vertical, while those in front slope backwards and those behind forwards. The centrum is short and thick, and bears at the front and hinder ends a small facet which, with that of the next vertebra, constitutes an articulating area for the head of the rib. In the last three or four this surface lies entirely on the anterior end of one centrum, and is not shared by the two. The transverse processes are well developed, and have an articular surface on their under face, for the tubercle of the rib: these facets are lacking from the last three or four vertebræ. On the neural arch of the ninth vertebra in the series a pair of slightly lateral wing-like processes passing dorsally appear. These are the **metapophyses,** and from the tenth onwards they are joined with the prezygapophyses.

The lumbar vertebræ possess stout centra; their neural spines are not so high, but are blade-like, and their metapophyses well developed. The transverse processes are short flattened rods projecting outwards and downwards. In addition to these other processes are also developed, the **hypapophyses,** triangular blade-like projections from the mid ventral line of the centrum, and the **anapophyses,** small short processes running backwards from the hinder end of the neural arch below the postzygapophyses but above the intervertebral notches.

The sacral vertebræ are all fused together, but, nevertheless, the lines of junction between them can be easily identified. Strictly speaking, only those vertebræ articulating with the ilia, generally one but at most two, can be termed the sacrum, but it is customary to apply the term to the whole of the vertebræ fused with them to form one mass.

The caudal vertebræ rapidly decrease in size and complexity, losing their processes, and even towards the end of the tail, their neural arches, so that the terminal members of the series are represented only by their rod-like centra.

Ribs and Sternum.

The ribs in the rabbit number twelve or sometimes thirteen pairs, and together with the backbone and the sternum constitute a bony basket in which lies the thorax. Each rib is a curved, somewhat flattened rod of bone passing out laterally and slightly backwards from the vertebral column. The dorsal end is enlarged to

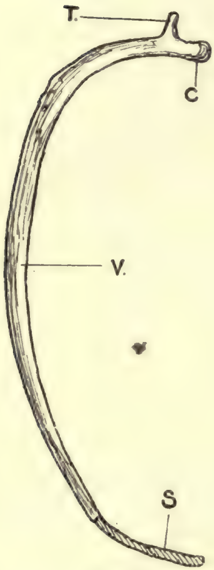


FIG. 89—Rib of *Lepus* viewed from anterior aspect.

C., capitulum; S., sternal portion; T., tuberculum; V., vertebral portion.

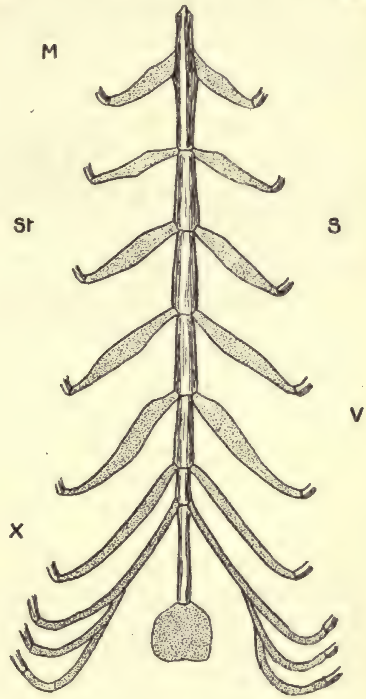


FIG. 90.—Sternum of *Lepus* from ventral surface.

M., manubrium; S., sternal portions of ribs; St., sternebræ; V., vertebral portions of ribs; X., xiphisternum.

form a knob-like head or **capitulum** which articulates with the facets on the centra. Just lateral to this is given off a dorsal projection, the **tuberculum,** which, as we have seen, articulates with a facet on the under side of the transverse process of a thoracic vertebra; but such a tubercle is absent on the posterior three or four pairs which have only a capitulum. To the lateral extremity of each bony **vertebral part** of the rib is attached a short bar of calcified or incompletely ossified cartilage, the **sternal portion,**

almost at right angles. This passes inwards towards the mid-ventral line The first seven pairs of these directly join the sternum, the next two almost reach it, and are each connected with the rib in front. The remaining pairs are not so complete and not so attached, and in consequence sometimes termed the floating ribs.

The **sternum** is a moderately wide flattened rod lying in the mid ventral line and divided into six segments, or **sternebræ**. The first, termed the **manubrium,** is larger than the rest and possesses a marked ventral ridge-like keel ; to it is joined the first pair of ribs. The posterior segments, the **xiphisternum,** is a long slender one, terminating in a thin flattened rounded cartilaginous plate. It has been found that in the embryo the sternebræ develop from the ventral ends of the ribs, and it is a matter of doubt whether they are to be regarded as strictly homologous with the segments of the sternum in *Rana.*

Skull.

The skull of a mammal is modified to adapt it for the acquisition of its food, and in the case of the rabbit, a **Rodent** or gnawing animal, this process of modification has been carried so far that it has resulted in a highly specialised structure that is considerably removed from what may be considered a generalised mammalian skull. For that reason it is better to study another form, say the dog, in order to get a general idea of the structure of a skull, and so it is only necessary here to refer to certain of its main features in the rabbit.

For the purposes of description we can divide the skull into a larger posterior cranial region and a smaller anterior facial region. At each side of the former, towards the front, lies a large hollow, the orbit, in which the eye is situated, while behind this the auditory capsule is actually fused with the cranium proper. The actual portion occupied by the brain case is relatively small, since in their middle regions the orbits are only separated by a thin bony partition, the **interorbital septum,** perforated by the optic foramen, and the brain does not extend directly in front of or below this. The various cartilage and membrane bones comprising the skull remain more or less distinct throughout life, being united along their edges by wavy junctions, the **sutures.** In the following account the cartilage and membrane bones will be distinguished by placing the letters c or m in brackets after their names.

The facial region consists mainly of an elongated nasal capsule. This is roofed by the paired somewhat long **nasal bones** (m) and its antero-lateral and ventro-lateral wells formed by the **premaxillæ** (m). Each premaxilla carries two **incisor teeth,** the anterior of

which is broad, long and curved and the posterior immediately behind it is rounder, smaller and less curved. The enamel layer is more strongly developed on the front than on the hinder edge of the anterior incisor, with the result that use keeps it sharpened as the hinder edge wears away quicker than the front, always preserving a chisel-like cutting surface. A long narrow continuation of the premaxilla, the **nasal process,** runs backwards alongside the nasal bone. The space left on the ventral side of the nasal capsule between the premaxillæ is in part filled by two median ventral

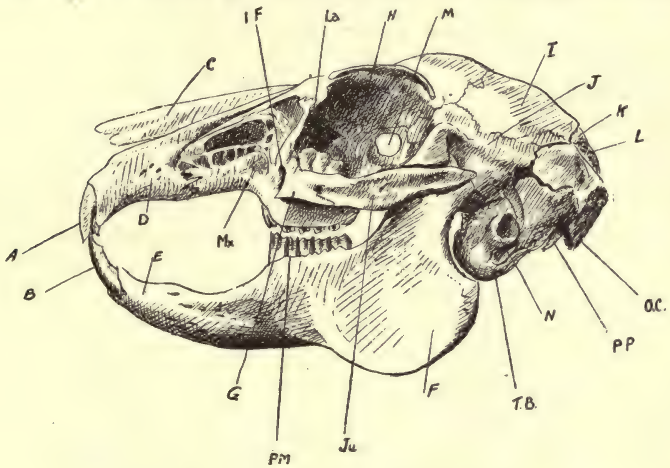


FIG. 91.—*Lepus*. Lateral view of skull.

A., superior incisor ; B., inferior incisor ; C., nasal ; D., pre-maxilla ; E., mandible ; F., angle of mandible ; G., zygomatic process of maxilla ; H., frontal ; I., parietal ; I.F., infra-orbital foramen ; J., squamosal ; Ju., jugal ; K., interparietal ; L., supra-occipital ; La., lachrymal ; M., optic foramen ; Mx., maxilla ; N., external auditory meatus ; O.C., occipital condyle ; P.P., paroccipital process ; Pr., premolar ; T.B., tympanic bulla.

backwardly running plates, the **palatine processes,** one from each premaxilla. At the hinder end the two nasal cavities are separated by a complete bony plate coming from the **mesethmoid bone** (c) and termed the **septum narium ;** this is continued in the living animal, to the front end of the cavities as a cartilaginous lamina which is generally absent in prepared skulls. Practically the whole of the nasal cavity on each side is filled by a number of extremely delicate much coiled bones, the **turbinals** (c), termed the **ethmo-turbinals, maxillo-turbinals** or **naso-turbinals** according to the bone to which they are attached. Much of the wall of the postero-lateral and postero-ventral regions of the olfactory capsule is completed by processes of the **maxilla** (m) proper, the main mass of which, however, lies in the cranial region.

The roof of the cranial region of the skull is composed of paired **frontal** (m) and **parietal** (m) bones and posteriorly by a small **interparietal** (m) bone. The frontals are large bones forming not only the roof but also the sides, and right in front also the floor of the brain case. In front they meet the nasals and behind the parietals. They send a very thin process forwards which separates the nasal process of the premaxilla from the maxilla for some distance, and again over each orbit they send out a prominent crescent-shaped **supra-orbital process.** The parietals are somewhat smaller bones meeting the frontals anteriorly, the interparietal and supra-occipitals posteriorly and the squamosals along the side. The median suture where the nasals, frontals and parietals of the two sides meet is termed the **sagittal suture.** The interparietal is a small oval bone bounded by the parietals in front and the supra-occipitals behind.

The side wall of the cranial region comprises a number of bones. At the antero-ventral end lies the **maxilla** (m). This is a complex bone whose main mass forms the upper jaw and bears a series of six teeth ; three are termed **pre-molars** and three **molars.** The two sets are, in *Lepus*, indistinguishable in structure and consequently all may be described as molariform. They are the grinding teeth and between them and the incisors there is a long gap, the **diastema.** Teeth corresponding with the canine teeth of other mammals are lacking. The antero-lateral plate of the maxilla, forming a large part of the side of the nasal capsule, is cancellous. On the ventral side the maxilla sends in a short stout **palatine process** which joins its fellow in the middle line, and these, with similar adjoining processes of the palatine bone, constitute the bony floor of the narial passage : this floor is the hard palate and forms also part of the roof of the mouth. From the side of the maxilla is given off a stout **zygomatic process,** which also continues upwards as an **orbital process** forming the front wall of the orbit. The remainder of the anterior orbital wall is completed by a small **lachrymal bone** (m) which is interpolated between the orbital process of the maxilla and the frontal bone and is perforated by a canal for the duct of the lachrymal gland. The inner wall of the orbit is completed by the **orbito-sphenoid** (c), **palatine** (m), **squamosal** (m) and the **alisphenoid** (c) bones. The **orbito-sphenoid** is a lamella of bone surrounding the orbital foramen ; it is bounded above by the frontal, in front by the maxilla, below by the palatine and behind by the squamosal. The **palatine** is an almost vertical plate of bone forming the side walls of the posterior end of the narial passage. At its front end it gives off a palatine process which, as we have seen, takes part in the formation of the hard palate. In addition, the palatine also forms the mid ventral part of the inner orbital wall where it joins the maxilla in

front and the alisphenoid behind. The **squamosal** is a large bone whose anterior portion takes part in the formation of the hinder wall of the orbit. Its lateral portion helps to form the side wall of the hinder region of the cranial cavity. Laterally it gives off a conspicuous **zygomatic process,** on the postero-ventral surface of which is a smooth facet for the articulation of the lower jaw. The **alisphenoid** is a wing-shaped bone, part of which is embedded in the posterior corner of the orbit. From its ventral border arises a small transversely lying plate of bone, the **external pterygoid process,** perforated by three holes ; the innermost is for the passage of the internal maxillary artery and vein and the outermost for branches of the mandibular trunk of the trigeminal nerve. At the innermost ventral corner of the alisphenoid bone is a large vertical slit, the **foramen lacerum anterium** or **sphenoidal fissure,** which permits the exit of the third, fourth and sixth cranial nerves and the first two branches of the fifth. The external lower border of the orbit is composed of the zygomatic processes of the maxilla and the squamosal and a thin strip of bone lying in the vertical plane, the **malar** or **jugal** (m), which joins them. The three structures together forming a curved **zygomatic arch** or **zygoma.**

The extreme front end of the cranial cavity is bounded by a vertical transverse plate of bone, the **mesethmoid** (c), which is not visible externally and completely separates the cranial and nasal cavities. The septum narium, already dealt with, is a median forward projection of this bone and its lateral wings, termed the **cribriform plates,** are perforated by a number of holes which transmit the various branches of the olfactory nerve.

The base of the cranial region between the palatines is formed by a thin vertical plate, the **presphenoid** (c), which forms the lower border of the orbital foramen. Within the skull, on the floor of the cranial cavity, it is produced into a small transverse **anterior clinoid process.** Immediately behind this bone is the **basisphenoid** (c), a median triangular fairly thick bone which is bounded laterally by the alisphenoids and posteriorly by the **basioccipital.** It is perforated in the mid-ventral line by a small hole, the **pituitary foramen.** On the inner floor of the cranial cavity it is produced upwards into a transverse **post-clinoid** process, and between this and the anterior process in a depression, the **sella turcica,** within which lies the pituitary body. Just at the junction of the basi and alisphenoid is attached a small, thin, vertical bone, the pterygoid, which is joined to the palatine in front and passes downwards in a free **hamular process.**

The auditory capsule is composed of a series of bones which in the adults fall into two portions, the **periotic** and the **tympanic.** The periotic is an irregular mass comprising developmentally three separate

elements, the **pro-otic,** the **epi-otic** and the **opisth-otic** and is divisible into two secondary regions, a very dense hard **petrous portion** enclosing the membranous labyrinth and a more cancellous **mastoid portion** which is visible on the outside of the skull and bounded posteriorly by the exoccipital bone. The surface of the periotic facing the inside of the cranium has a deep pit-like depression, the **floccular fossa,** in which is contained a projecting portion of the cerebellum termed the floccular lobe. Below this are two openings side by side ; the hinder one is the **meatus auditorius internus** through which the auditory nerve passes from the brain to the inner ear, and the other foramen is the **aquæductus Fallopii,** transmitting the facial nerve. The outer surface of the petrous portion is perforated by two holes which, however, cannot be seen until the tympanic bone has been removed. The anterior one is the **fenestra ovalis** and the posterior one is the **fenestra rotunda ;** both lead to the internal ear from the tympanic cavity. The hollow tympanic bone has the shape of a short-necked flask. Its expanded part, termed the **bulla,** contains the tympanic cavity, while the neck is the **meatus auditorius externus** or external ear aperture. Across the base of the meatus in life lies the tympanic membrane, which is tightly stretched over an incomplete bony ring. The Eustachian tube leaves the tympanic cavity by an aperture at the antero-ventral corner of the tympanic bulla and opens into the posterior part of the narial passage. Just next to this, between the tympanic bone and the alisphenoid, is the **foramen lacerum medium** for the transmission of the mandibular branch of the trigeminal nerve. On the postero-ventral aspect of the bulla is a round foramen through which the internal carotid artery passes into the cranial cavity. Between the postero-lateral border of the bulla and the mastoid portion of the periotic is the **stylomastoid foramen,** through which runs the main branches of the facial nerve. Across the tympanic cavity stretches a string of bones termed collectively the auditory ossicles. The outermost of these, the **malleus** (c), is a hammer-shaped bone with its blade-like handle attached to the tympanic membrane and also articulating with the second bone, the **incus** (c). This is a pyriform bone produced behind into a short process and below into a short stalk bent inwards. To the end of this is attached a small disc of bone, the **os orbiculare** (c), which in turn articulates with the arch of a stirrup-shaped bone, the **stapes** (c). The basal oval-shaped part of this bone is attached to the membrane closing the fenestra ovalis. By means of this chain of bones the vibrations of the tympanic membrane are transmitted to the perilymph surrounding the membranous labyrinth.

The posterior end of the cranial region is composed of a ring of four bones, termed the **occipital segment.** The dorsal member is

the **supra-occipital** (c), a large median bone joining the parietals in front, the squamosals and periotics at the side and the exoccipitals ventro-laterally, while its mid ventral portion forms part of the wall of the foramen magnum. Its postero-dorsal portion is marked by strong ridges into which are inserted the muscles raising the head. The lateral bones are the **exoccipitals** (c), which form the major part of the wall of the foramen magnum. They bear posteriorly strong curved smooth ridges, the **occipital condyles,** which articulate with the condylar facets of the atlas. Laterally each bone is produced downwards as a **paroccipital process** behind the periotic bone. Between the posterior border of the tympanic bulla and the exoccipital is an irregular fissure, the **foramen lacerum posterius,** through which passes the ninth, tenth and eleventh cranial nerves and the internal jugular vein. The twelfth nerve leaves the cranium by two branches which pass through the body of the condyle, and the condylar foramina that transmit them are best seen on the inside of the condyles. The basal part of this ring of bones is completed by a large **basioccipital** (c) ; it forms the ventral wall of the foramen magnum and contributes a small part of each condyle.

The lower jaw or **mandible** (m) consists of a pair of flattened triangular masses of bone, thin and broad posteriorly, but getting thicker and narrower as they pass forward till they finally unite in the **symphysis menti.** At the anterior end each half or **ramus** bears a single incisor tooth ; this is followed by a diastema, and this by two premolars and three molars all molariform and similar to those in the upper jaw. Each ramus gives off posteriorly a broad, thin ascending **coronoid process** which passes up to articulate, by means of a transverse expansion of its upper end, with the under side of the zygomatic process of the squamosal. The postero-ventral border of the ramus is known as the **angle** and its edge is slightly incurved. On the inner side of each ramus just behind and below the last molar tooth is an aperture, the **inferior dental foramen,** through which a branch of the mandibular nerve enters the bone to supply the teeth.

The **hyoid bone** (c) is a small bone embedded in the muscles of the base of the tongue between the hinder ends of the rami. It possesses a body and two pairs of **cornua.** The **anterior cornua** represent the persistent remains of the hyoid arch of the embryo and the **posterior cornua,** also termed **thyrohyals,** the lower ends of the first branchial arch.

Appendicular Skeleton.

We now pass on to consider the remaining part of the skeleton comprising the pectoral and pelvic girdles and the fore and hind limbs. All of its main bones are cartilage bones save

only the clavicle which is a membrane bone, but in addition there are also developed in certain of the tendons, sesamoid bones.

Pectoral Girdle.

Compared with *Rana* we find the pectoral girdle much reduced and consisting mainly of two elements, a dorsal and a

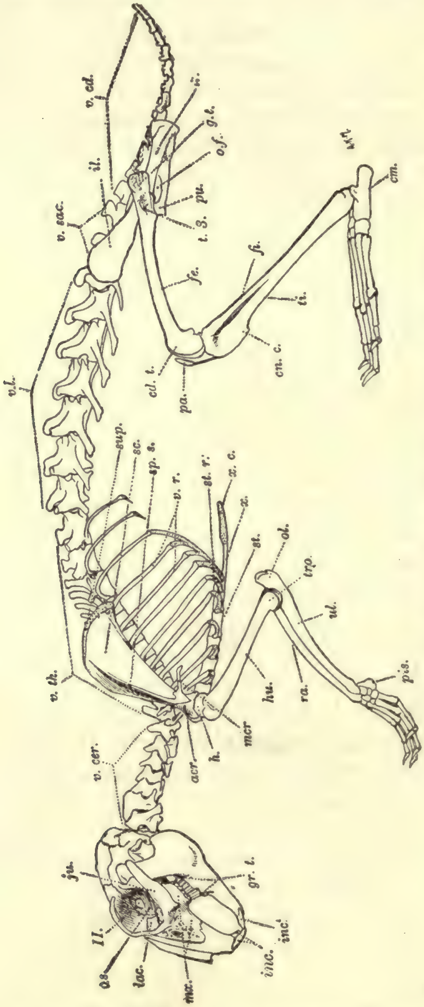


FIG. 92.—The skeleton of a rabbit.—From Borrodaile.

acr., acromion; *cd.t.*, condyles for tibia; *cm.*, calcaneus; *cn.c.*, cnemial crest; *fe.*, shaft of femur; *fi.*, fibula; *g.t.*, great trochanter; *gr.t.*, premolar and molar teeth; *h.*, head of humerus, fitting into glenoid cavity; *hu.*, shaft of humerus; *il.*, ilium; *inc.*, upper incisor teeth of the left side; *inc'.*, lower incisor tooth; *ju.*, jugal bone; *lac.*, lachrymal bone; *mcr.*, metacromion; *mx.*, maxilla; *o.f.*, obturator foramen; *ol.*, olecranon process; *os.*, orbitosphenoid bone; *pa.*, knee-cap; *pis.*, pisiform bone; *pu.*, pubis; *ra.*, radius; *sc.*, scapula; *sp.s.*, spine of scapula; *st.*, sternum; *st.r.*, sternal ribs; *sup.*, suprascapula; *t.3*, third trochanter; *ti.*, tibia; *tro.*, trochlea; *ul.*, ulna; *v.cd.*, *v.cer.*, *v.l.*, *v.sac.*, *v.th.*, caudal, cervical, lumbar, sacral and thoracic regions of the backbone; *vr.*, vertebral ribs; *x.*, xiphisternum; *x.c.*, xiphoid cartilage; *II.*, foramen for optic nerve.

ventral. The **scapula,** or shoulder blade, is a thin flat triangular plate of bone. The apex of the triangle bearing the **glenoid facet,** lies laterally over the first rib and the remainder passes back dorsally

towards the middle line. The bone is thickened in the region of the glenoid facet which bears on its edge a small inwardly projecting **coracoid process,** the representative of part of the coracoid portion of the girdle of the frog. The outer surface of the scapula bears a prominent keel-shaped **spine** which increases in depth as it passes to the glenoid facet. Just before reaching this it becomes free from the plate and continues as a slender flattened rod, the **acromion,** from the end of which is given off at right angles a backwardly projecting process, the **metacromion**. The supra-scapula of the frog is represented in *Lepus* by a cartilaginous **supra-scapular border** attached to the dorsal edge of the scapula. The **clavicle** or collar bone of the rabbit is a small slender curved rod of bone attached by fibrous tissue to the coracoid process at the one end and to the sternum at the other.

Pelvic Girdle.

As in the frog, the pelvic girdle has undergone a rotation from its original plane, until instead of being approximately at

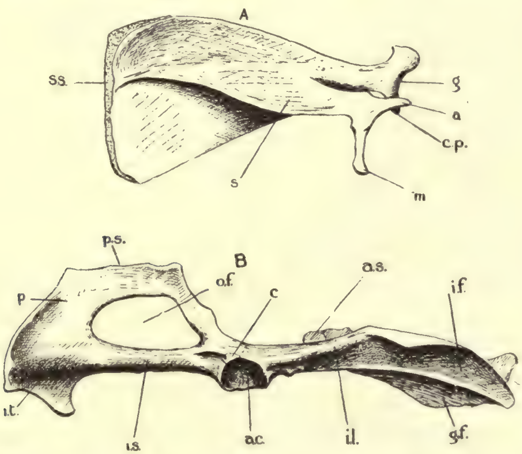


FIG. 93.—A, Right scapula of *Lepus*, dorsal aspect; B, Left os innominatum *Lepus*, ventral aspect.

a., acromion; *ac.*, acetabulum; *a.s.*, articular surface for sacrum; *c.*, cotyloid; *c.p.*, coracoid process; *g.*, glenoid facet; *g.f.*, gluteal fossa; *i.f.*, iliac fossa; *il.*, ilium; *is.*, ischium; *i.t.*, ischia tuberosity; *m.*, metacromion; *o.f.*, obturator foramen; *p.*, pubis; *p.s.*, pubic symphysis; *s.*, spine; *s.s.*, supra-scapular cartilage.

right angles to the vertebral column it comes to lie almost parallel with it. The girdle is composed of two halves only feebly united in the mid-ventral line; each is roughly in the form of a P, and is termed the **os innominatum.** This, however, really consists of

three elements, the **ilium,** the **ischium** and the **pubis,** closely fused together and all taking part in the formation of the **acetabulum,** a deep cavity in which the head of the femur articulates. The **ilium** is the anterior dorsal bone of the girdle on each side and is flattened in the vertical plane. Its inner, **sacral surface,** is roughened for junction with the sacrum. The outer surface is marked by a longitudinal ridge, leaving a shallow dorsal depression, the **gluteal fossa,** and a similar ventral one, the **iliac fossa.** It forms about one-half of the acetabulum. The **ischium** is the second largest bone in the girdle passing backwards from the acetabular cavity, of which it forms about one-third, in the same line as the ilium. About half-way back it gives off dorsally a blunt **ischial spine** and it terminates in an expanded roughened enlargement, the **ischial tuberosity.** The smallest bone is the **pubis,** whose contribution to the acetabulum, less than one-third, usually ossifies separately and is termed the **cotyloid bone.** It passes ventrally as a thin strip of bone to meet its fellow in the middle line in the **pubic symphysis,** continuing this union backwards until it joins the inner portion of the expanded end of the ischium. Save for this posterior junction, only visible in young animals, the pubis and ischium are separated by a large hole, the **obturator foramen.**

Fore Limb.

The fore limb of the rabbit is composed of the same main divisions as in the frog, but it is more highly specialised, and it differs considerably in the details of its structure.

The **humerus** is a long bone with a well-developed rounded **head,** articulating with the glenoid facet of the scapula, and an enlargement, the **trochlea,** at its distal end articulating with the radius and ulna. Near the head are two roughened projections, an **outer** or **greater tuberosity**, and an **inner** or **lesser tuberosity,** and they are separated by a **bicipital groove** for the tendrons of the biceps muscle. The trochlea is a ridged pulley-like surface just above which on each side is a deep **supra trochlear fossa,** and these two fossæ communicate with one another by means of a **supra trochlear foramen.** The posterior of the two is considerably the larger and often termed the **olecranon fossa,** since it lodges part of the olecranon process when the arm is fully extended. The **radius** and **ulna** are almost of equal size, and although not actually fused are immovably articulated. The **radius** is the inner bone and articulates proximally with the trochlear notches, while distally, where it is somewhat enlarged, it touches the carpal bones. The **ulna** has a small distal end, but its **proximal** extremity is enlarged and marked by a deep groove, the **sigmoid notch,** in which lies part of the trochlea, while it is continued

on beyond the joint as a laterally compressed **olecranon process.** The **carpus** or wrist consists of nine bones. The three proximal carpalia, *i.e.* the radiale, intermedium and ulnare, are three small bones articulating with the radius and ulna and sometimes termed the **navicular** (scaphoid), **lunate** (semilunar) and **triquetral** (cuneiform) respectively. The distal carpalia in order from the radial to the ulnar side are the **greater multangular** (trapezium), the **lesser multangular** (trapezoid), the **capitate** (os magnum), and the **hamate** (cuneiform); the last named representing the fusion of two separate elements. Between the proximal and distal carpalia lies another small bone, the **centrale,** and on the under side of the carpus articulating with the ulna and navicular is a small **pisiform** bone usually regarded as being a sesamoid bone. There are five metacarpals, of which the first is markedly smaller than the rest. The digits are also five in number, of which the innermost, the thumb or pollex, is much shorter than the others, possessing only two phalanges as against three in the remainder.

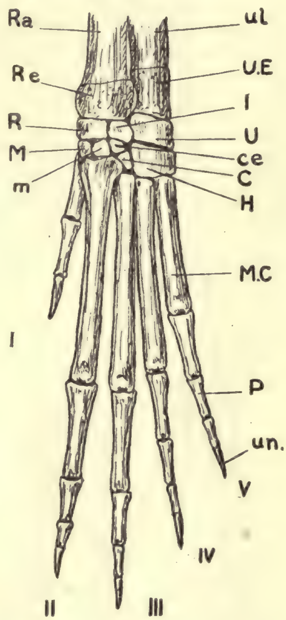


FIG. 94.—Left fore foot of *Lepus* viewed from extensor surface.

C., capitate; Ce., centrale; H., hamate; I., intermedium; M., great multangular; *m.*, lesser multangular; M.C., metacarpal; P., phalanx; R., radiale, navicular; Ra., radius; R.E., epiphysis of radius; U., ulnare, triquetral; U.E., epiphysis of ulna; Ul., ulna; Un., ungual phalanx; I., pollex; II.-V., digits.

Hind Limb.

The hind limb is noticeably larger than the fore limb and plays a far more important part in locomotion.

The **femur** is a long bone with a cylindrical shaft and two enlarged extremities. On the inner side of the proximal end is a large projecting rounded **head** which lies partly enclosed within the acetabular cavity. On the outer side of the proximal end, opposite the femur, is a large rough mass, the **great trochanter,** and between that and the head on the hinder side is a deep **trochanteric fossa.** Just below the head are two smaller projections, one on each side; that on the inside being the **lesser trochanter** and that on the outside the **third trochanter.** The distal end of the bone is swollen out to form two large condyles separated by an **intercondylar notch**; it articulates with the tibia and fibula. Over, the front of this joint

lies a large sesamoid bone, the **patella** or knee-cap, and behind it are another series of small bones, the **fabellæ**.

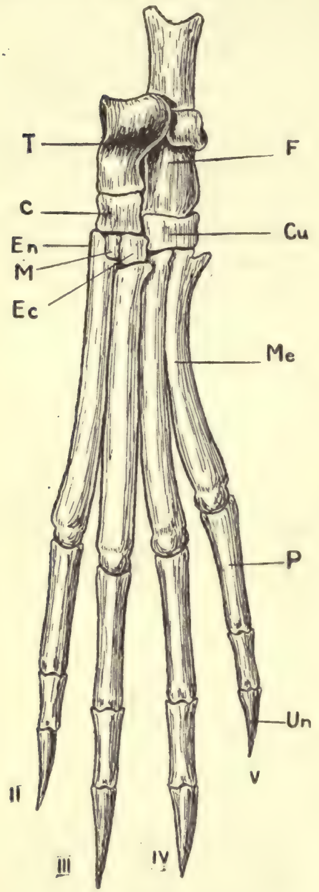


FIG. 95—Left hind foot of *Lepus*, viewed from extensor surface.

C., centrale, navicular; Cu., cuboid; Ec., ecto-cuneiform; En., process probably representing ento-cuneiform; F., fibiale, calcaneum; M., meso-cuneiform; Me., metatarsal; P., phalanx; T., talus = tibiale + intermedium; Un., ungual phalanx; II.-V., digits.

The tibia and fibula are two long bones, the former much larger than the latter, which are free proximally but fused distally. The **tibia** is a long stout bone with an enlarged proximal extremity for articulation with the femur and bearing on its anterior surface a prominent **cnemial crest,** while its distal end articulates with the talus. The **fibula** is a slender bone, free proximally but fusing distally with the tibia and also bearing a facet for articulation with the calcaneum. The tarsalia in *Lepus* have been reduced to six bones. The proximal row consists of two bones, of which the inner represents the tibiale and intermedium fused and is often termed the **talus**, while the outer or fibulare is termed the **calcaneum.** The **centrale** or **navicular** is a bone continuing the line of the talus and sending forward a slender process on the under surface of the foot. There are but three distal carpalia, the first or **ento-cuneiform** is altogether lacking as a separate element, but is probably fused with the second metatarsal so that the innermost is really the second or **meso-cuneiform**; the next is the third **ecto-cuneiform** and the remaining bone represents two tarsalia fused, and is termed the **cuboid.** Only four metatarsals are present, the first, corresponding with the metatarsal of our big toe, is absent, as indeed is the whole toe. The remainder are long bones, the innermost bearing a backwardly projecting corner which, as has just been pointed out, is probably the innermost distal tarsal. Each metatarsal is followed by a digit composed of three phalanges.

The distal phalanges in both fore and hind limbs are of a characteristic bent pointed shape, and are covered by the hollow horny claws so that they are termed the **ungual phalanges.**

The Pentadactyl Limb.

Having now studied the fore and hind limbs of both frog and rabbit we are in a position to consider the relation of one to the other and to the limbs of air-breathing vertebrates in general.

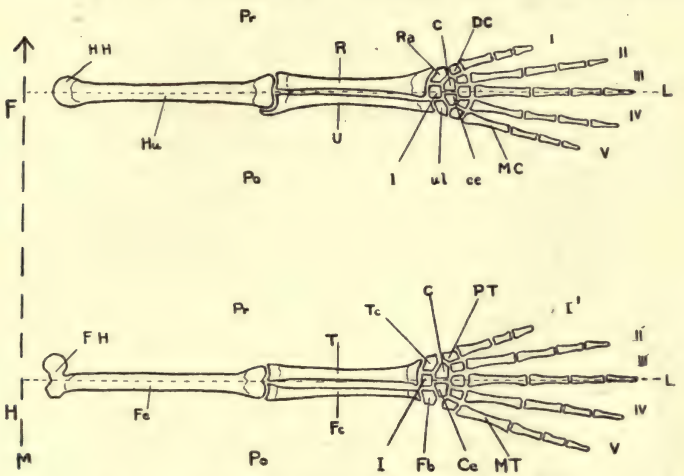


FIG. 96.—Idealised diagram of pentadactyl limbs.

C., pre-axial centrale ; Ce., post-axial centrale ; D.C., distal carpalia ; D.T., distal tarsalia ; F., fore limb ; Fb., fibulare ; Fe., femur ; F.H., head of femur ; Fi., fibulare ; H., hind limb ; H.H., head of humerus ; Hu., humerus ; I., intermedium ; L., axis of limb ; M., main axis of body ; M.C., metacarpal ; M.T., metatarsal ; Po., post-axial border of limb ; Pr., pre-axial border of limb ; R., radius ; Ra., radiale ; T., tibia ; Ti., tibiale ; U., ulna ; Ul., ulnare ; I., pollex ; I'., hallux ; II.-V., digits.

Comparison will show that not only are the fore and hind limbs in each animal composed of homologous parts, but also that there is a fundamental similarity between those of *Lepus* and *Rana*. Indeed, we can go further than this and sketch the plan of a primitive limb from which most probably those of all vertebrates in the classes Amphibia, Reptilia, Aves and Mammalia have been derived and of which they can certainly be regarded as modifications. This ideal type is known as the typical pentadactyl limb and is constituted in the following way. The proximal element is a long cylindrical bone, the humerus or femur, enlarged proximally to form a head for articulation with the girdle and enlarged distally for articulation with the succeeding elements. The next portion is composed of two bones, a radius and ulna or a tibia and fibula, which articulate

distally with the groups of bones forming the carpus or tarsus as the case may be. These groups consist primitively of ten bones arranged in three rows. The first or proximal row comprises three bones, the radiale and ulnare or the tibiale and fibulare, articulating with the correspondingly named limb bones, and between them in each case is the third element, an intermedium. The second row consists of two central bones, the centralia ; in most animals but one of these is represented either freely or fused, but there is evidence to show that primitively there were two. In the distal row are five bones, the distal carpalia or tarsalia, and again there is frequently loss or fusion of these. Each of them is followed by a metacarpal or metatarsal, which are longer bones contained within the palm of the hand or sole of the foot. Following these are the five digits composed of a series of phalanges. In each case the first digit, the thumb or pollex and the big toe or hallux, is shorter than the remainder and composed of but two phalanges, whereas the others are each composed of three. This, then, is the structure of the primitive pentadactyl limb, but it also has definite relations to the body as a whole. In its original position, when extended, it was related to the main or vertebral axis in the same way as our own arm would be if it were held straight out to the side at right angles to the body with the thumb uppermost. An imaginary line drawn lengthwise through the limb, *i.e.* through the proximal bone, the intermedium and the middle digit, is regarded as the **axis** of the limb. The parts of the limb on the same side as the radius and pollex or tibia and hallux are termed **pre-axial,** those on the opposite side *e.g.* ulna or fibula, etc., are **post-axial.** The digits are numbered one to five from the preaxial side, and so we have in both limbs a phalangeal formula of 2.3.3.3.3. In the primitive animals this was the position of the limbs which were, however, bent or flexed at right angles at the elbow or knee so as to allow the palm of the hand or sole of the foot to reach the ground. The surface on the inner side of the bend is termed the flexor surface, while that on the outer side is the extensor surface. However, in the rabbit and in mammals generally the limbs have undergone a certain amount of rotation. Taking the arm from the position just described and swinging it to the front, still at right angles to the body, it will be seen that in order for the palm of the hand to touch the ground it is necessary to turn the hand, and with it the forearm, through an angle of 90° so that the thumb, instead of pointing upwards, points inwards and the palm downwards. In this position the hand is said to be in **pronation**, while in the original position it is in **supination.** The fore limb of *Lepus* therefore is permanently in a position of pronation, *i.e.* the forearm and hand are twisted with regard to the arm.

The bringing of the hallux to the inside of the hind limb is not accomplished in the same way, but this is done by the rotation of the limb as a whole, whereby the original dorsal border becomes the anterior border, but there is no extra twisting of the lower part of the limb.

This ideal type of limb is only met with in a few primitive animals and in all others a certain, often very considerable, amount of modification has occurred. One of the first changes is a fusion or loss of certain of the carpal and tarsal elements, and another common one is a loss or reduction of the digits.

The Skull of a Mammal—The Dog, *Canis familiaris.*

For the study of a typical mammalian skull we may take that of the dog which, although not ideal, is fairly generalised and readily obtainable. While it is to the dog's skull that the details of the following description apply, it is well to bear in mind that the skull of all the higher Mammalia is constructed upon the same general plan and the differences are mainly small points, and particularly in the relative sizes of the parts. As in the frog, the skull of the mammal is first laid down in cartilage. In the adult it comes to consist of certain parts of this chondrocranium that have ossified and so became cartilage bones, to which have been added other membrane bones laid down in the surrounding tissues. Again, in *Canis* as in *Rana* the entire skull consists of the cranium or brain case, the olfactory, optic and auditory capsules, the upper and lower jaws and the hyoid apparatus, and to faciliate description we may deal with these various parts separately. The various bones in an old skull are closely joined together by small interlocking projections so that the line of union is indicated by wavy lines termed **sutures,** or it may be that they are so closely fused as to be indistinguishable. For purposes of study, therefore, it is well to examine a moderately young specimen.

Cranium.—The cranium is a large, hollow box somewhat oval in shape and occupying slightly more than the posterior half of the skull. The floor or base is more or less straight, while the roof is well arched. In the hinder part of adult skulls we find a prominent ridge in the mid-dorsal line; it is termed the **sagittal crest** and furnishes attachment for the large temporal muscles moving the lower jaw. The bones composing the cranium will be found to fall into three segments corresponding with three median, unpaired bones, namely, the basi-occipital, the basi-sphenoid and the presphenoid, which together form the basi-cranial region of the skull.

The occipital segment is composed of cartilage bones of which the mid-ventral is the **basi-occipital**, a flat plate at the hinder end

of the floor of the skull ending freely behind where it forms the ventral boundary of the **foramen magnum,** the large aperture

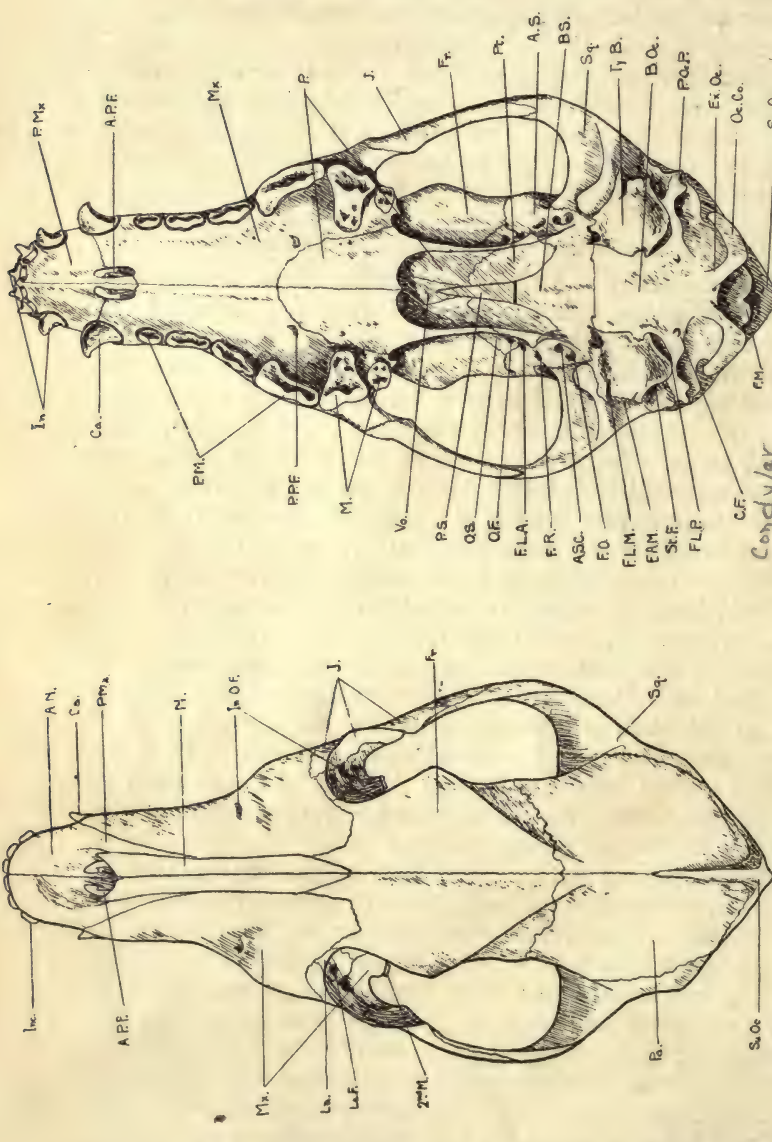


FIG. 97.—Dorsal view. Skull of dog, *Canis familiaris*. FIG. 98.—Ventral view.

A.N., anterior nares; A.P.F., anterior palatine foramen; A.S., alisphenoid; A.S.C., alisphenoid canal; B.Oc., basi-occipital; B.S., basi-sphenoid; Ca., canine; C.F., carotid foramen; E.A.M., external auditory meatus; Ex.Oc., ex-occipital; F.L.A., foramen lacerum anterius; F.L.M., foramen lacerum medium; F.L.P., foramen lacerum posterius; F.O., foramen ovale; F.M., foramen magnum; F.R., foramen rotundum; Fr., frontal; Inc., incisors; Inf.O.F., infra-orbital foramen; J., jugal; La., lachrymal; La.F., lachrymal foramen; M., molars; Mx., maxilla; 2nd.M., second molar; N., nasal; Oc.Co., occipital condyle; O.F., optic foramen; O.S., orbito-sphenoid; P., palatine; Pa., parietal; P.M., pre-molars; P.Mx., pre-maxilla; P.Oc.P., par-occipital process; P.P.F., post-palatine foramen; P.S., pre-sphenoid; Pt., pterygoid; Sq., squamosal; St.F., stylomastoid foramen; Su.Oc., supra-occipital; Ty.B., tympanic bulla; Vo., vomer.

through which the medulla passes backwards to become continuous with the spinal cord. Lying latero-dorsally on each side of this

are the **ex-occipital** bones, which form the larger part of the circumference of the foramen. Each has its hinder margin produced into a well-marked curved **occipital condyle,** which serves for articulation with the atlas or first vertebra. A large **occipital** sinus lies within the condyle, and its anterior and posterior openings show clearly inside the brain case. At its antero-lateral margin the bone is produced ventrally into a strong **par-occipital** process, giving a surface for muscle attachment, and internal to this it is perforated by a small hole, the **condylar** foramen, which is the exit for the hypogossal nerve. The line of junction between the basi- and ex-occipital bones is obliterated in the adult skull, but clearly visible in young examples. The dorsal border of the foramen magnum is formed by a median bone, the **supra-occipital,** constituting the flat, almost vertical plate at the hinder end of the cranium. In an old dog it is completely fused with a forward prolongation that appears as a median dorsal tongue of bone which, however, ossifies separately, and in some animals remains throughout life a distinct membrane bone, the **interparietal.**

The mid-ventral unit of the parietal segment is the **basi-sphenoid,** a flat plate of somewhat thicker cartilage bone more or less cancellous within. Ventrally it is fairly level, but inside the cranium it is hollowed in the middle to form a depression, the **sella turica,** in which lies the pituitary body. In some mammals its floor is perforated by a small opening, the **pituitary foramen,** which is not present in *Canis*. From the sides of this, extending upwards and outwards, arise the wing-like **alisphenoids,** also cartilage bones. Ventrally this bone gives off a vertical bony plate, the **external pterygoid process,** to the inner edge of which is attached the palatine bone. The alisphenoid itself is important because of the perforations or foramina connected with it. The base of the pterygoid process is pierced by the **alisphenoid canal,** through which the external carotid artery runs. The lower anterior margin of the portion of the alisphenoid in the orbit forms the posterior limit of a well-marked aperture running vertically, the **foramen lacerum anterius.** Through this pass the third, fourth and sixth cranial nerves supplying the muscles of the eye and also the ophthalmic branch of the fifth nerve. In its basal region the alisphenoid is perforated by two openings ; one is approximately round, the **foramen rotundum,** serving for the exit of the maxillary branch of the fifth nerve, and the other a slightly larger, oval, more posterior hole, the **foramen ovale,** for the mandibular branch of the trigeminal. The dorsal portion of the cranium in this region is formed by the large square-shaped membrane bones, the **parietals,** meeting in the middle line in a junction termed the **sagittal suture,**

save at the hinder end where they are separated by the interparietal portion of the supra-occipital.

Encasing the anterior end of the brain is the frontal segment whose median, basal cartilage bone is the **pre-sphenoid.** It is a narrow bone flat ventrally, but of irregular outline within the cranium; inside it is cancellous. Internally it just touches the lower border of the **optic foramen.** To the side of the pre-sphenoids are attached the thin wing-like **orbito-sphenoids,** also cartilage bones. They form part of the inner wall of the orbit and contribute the greater part of the margin of the **optic foramen.** At their posterior corner they also participate in forming the front border of the foramen lacerum anterius. Dorsally the cranial roof is composed of the large membrane bones, the **frontals,** which not only meet in the middle line continuing the sagittal suture, but also pass forwards and ventrally for some distance. Dorso-laterally the frontal bone gives off a projection, the **post-orbital process,** extremely well developed in some other mammals, which marks the hinder limit of the orbit. When the skull is viewed from above a large arch, the **jugal or malar arch** is seen to sweep out on each side of the cranium. The space within this arch may be divided into two, the so-called **orbital fossa,**lodging the eye in front, and the **temporal fossa,** which is filled in life by the great temporal muscle whose origin on the sagittal crest has already been noted.

Finally, the space at the front end of the cranium between the pre-sphenoid and the frontals is closed in by a median vertical plate of spongy cartilage bone, the **ethnoid.** Lateral expansions of this form the **cribriform plates,** which are vertical bones perforated by a large number of holes for the passage of numerous olfactory nerves. The bone itself is continued forward in the middle line as a thin vertical lamina, the **mesethmoidal plate** or **septum narium,** part of which always remains cartilaginous, and this separates the two olfactory capsules.

The front part of the skull, occupying less than half its length, consists in the main of the olfactory capsules and the bones connected with it. The capsule consists of an upper space, the olfactory chamber, and a lower tube-like portion, the narial passage. The roof of these capsules is made partly of prolongations of the frontal bones, the **nasal processes,** but mainly of two long narrow membrane bones, the **nasals,** whose front ends form the dorsal limit of the anterior nares. Their floor in the mid-ventral line is composed of a small elongated membrane bone, the **vomer,** representing a pair of bones fused. The remaining bones participating in the formation of the nasal capsule, namely, the palatines, maxillæ and pre-maxillæ, are better dealt with in

connection with the upper jaw and, as already noted, its hinder limit

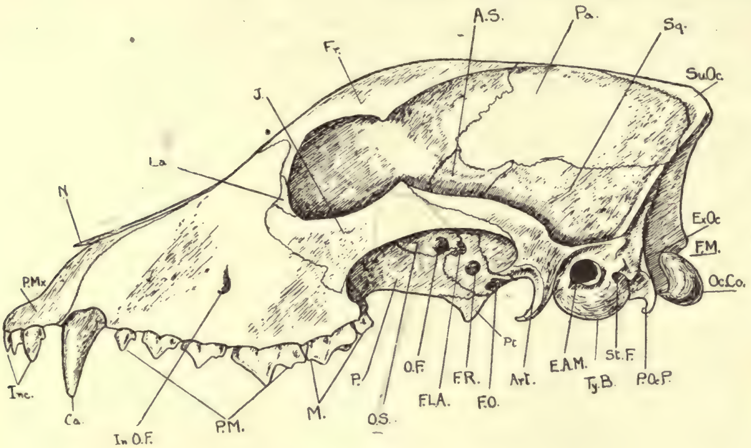


FIG. 99.—Lateral view.

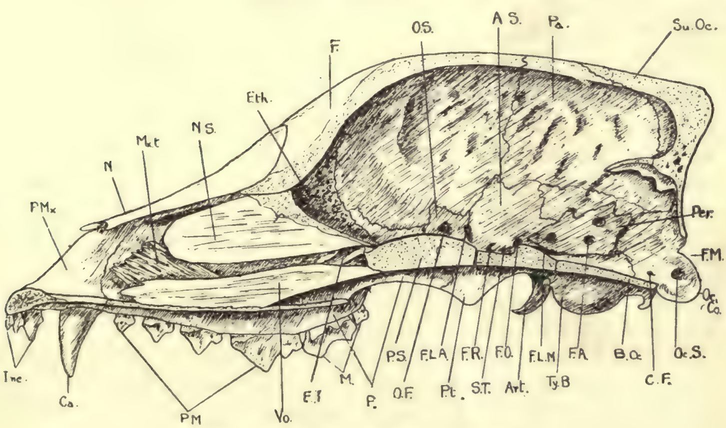


FIG. 100.—Medium long section.

Skull of dog, *Canis familiaris*.

Art., articular facet for lower jaw; A.S., alisphenoid; B.Oc., basi-occipital; Ca., canine; C.F., carotid foramen; E.A.M., external auditory meatus; E.T., ethmo-turbinals; Eth., ethmoid; Ex.Oc., ex-occipital; F.A., internal auditory foramen; F.L.A., foramen lacerum anterius; F.L.M., foramen lacerum medium; F.O., foramen ovale; F.M., foramen magnum; F.R., Foramen rotundum; Fr., frontal; Inc., incisors; Inf.O.F., infra-orbital foramen; J., jugal; La., lachrymal; M., molars; Mx.T., maxillo-turbinals; N., nasal; N.S., nasal septum; Oc.Co., occipital condyle; Oc.S., occipital sinus; O.F., optic foramen; O.S., orbito-sphenoid; P., palatine; Pa., Parietal; Per., peri-otic; P.M., pre-molars; P.Mx., pre-maxilla; P.Oc.P., par-occipital process; P.S., pre-sphenoid; Pt., pterygoid; Sq., squamosal; S.T., sella turica; St.F., stylomastoid foramen; Su.Oc., supra-occipital; Ty.B., tympanic bulla; Vo., vomer.

is marked by the cribriform plate. The main part of the posterior end of the cavity of the capsule is filled by a very complexly folded

and coiled series of bony lamellæ consituting the so-called **ethno-turbinal** bones, since they are fused behind with the ethmoid bone. They are covered by the olfactory membrane, which is well supplied with sense cells and nerves, and so serve to provide a much greater area for the sensory epithelium than would be possible without the folding. The most dorsal of these lamellæ lie close to the nasal bones with which they become fused in some mammals, and then they are termed the **naso-turbinals.** A similar series of even more slender lamellæ are to be found in the anterior part of the nasal cavity, and as they are fused with the maxillæ they are distinguished as the **maxillo-turbinals.**

The optic capsule, well developed in bony fishes, is very much reduced in the mammal and comes to consist of a single membrane bone, the **lachrymal,** on each side. This is a small bone lying on the anterior border of the orbit at the ventral limit of the junction between the frontal bone and the maxilla. It is perforated by the **lachrymal foramen,** through which passes the duct of the lachrymal or tear gland. In some mammals it is but loosely attached to the surrounding bones, but in the dog it is more firmly inserted.

The auditory capsule consists of a group of bones more or less firmly joined together and lying laterally to the basi-occipital and immediately in front of the par-occipital process. The most obvious part externally is the **tympanic,** a cartilage bone which is swollen out ventrally to form the well-marked **tympanic bulla.** At the hinder median border of the bulla lies an obliquely directed aperture, the **foramen lacerum posterius,** through which the ninth, tenth and eleventh cranial nerves leave the skull in company with the internal jugular vein. Behind its postero-dorsal corner is a somewhat round hole, the **stylomastoid foramen,** serving for the exit of the main part of the seventh cranial nerve. Antero-laterally to the bulla lies an irregular opening, the **foramen lacerum medium,** which on closer examination is seen to be double. The more median of the two perforations is the **foramen caroticum,** through which the internal carotid artery reaches the brain and slightly to the outside of this is the orifice of the **Eustachian canal** for the Eustachian tube. On its anterior, upper surface the tympanic bone is produced into a short neck with a wide opening, the **external auditory meatus.** Across the bottom of the neck in life is stretched the tympanic membrane supported by an incomplete bony ring.

The internal portion of the auditory capsule is formed by an irregular cartilage bone, the **peri-otic,** which is regarded as being composed of three separate elements, the pro-otic, the epi-otic and the opisth-otic, and lodges the internal ear. In the adult the single bone formed by this fusion can be divided into two more or less

well-marked parts, the **petrous portion** on the inside and the **mastoid,** which is produced posteriorly into a **mastoid process** lying next to the par-occipital process. An oval opening, the internal auditory meatus, lies on the middle of the inner surface of the per-iotic bone ; into this go the eighth nerve supplying the internal ear and the seventh nerve which reaches the outside of the skull through the stylomastoid foramen, as has been noted above. On the outer surface of the peri-otic bone facing the tympanic cavity, and so not seen unless the tympanic bulla is removed, are two small holes, the **fenestra ovalis** and **fenestra rotunda,** which place the inner ear in communication with the cavity. Within and stretching across the tympanic cavity itself is a chain of small bones connected with the function of hearing. The **malleus** is a small bone consisting of a blade-like portion, the manubrium, which is attached to the tympanic membrane, and a more solid body. The latter part articulates with the next bone in the series, the **incus,** and this also has a tiny process, the end of which fits on to a small bony disc, the **os orbiculare.** The last bone, the **stapes,** is shaped somewhat like a stirrup with a central perforation. At one end it joins the os orbiculare and the other is flattened to form a basal plate that closes the fenestra ovalis.

To turn now to the jaws, which although laid down in cartilage in the embryo, are entirely replaced by membrane bones in the adult.

The **pterygoids** are thin lamellæ of bone lying almost in the vertical plane ; their bases lie upon the pre-sphenoid and basi-sphenoid, laterally they pass downwards on the inside of the alisphenoid to which they are closely apposed and they project freely beyond this for a short distance only. Thus in looking at the skull from the side only the small triangular points of these bones are visible. At their anterior end they are attached to the next bone in the series, the **palatine.** This is an irregular and much larger bone. Its lateral portion which abuts on to the pterygoid continues upwards and outwards to form a considerable part of the antero-ventral wall of the orbit, where it articulates with the alisphenoid behind, and the orbito-sphenoid and frontal above. It stretches forward to the lachrymal and contributes partly to the mesial margin of the hinder opening of the infra-orbital canal. Later in its orbital region it joins the maxilla. Near the line of junction with the maxilla lie two small perforations in the palatine bone. The upper of these leads into the narial passage and transmits the posterior nasal branch of the trigeminal, while the lower is for the palatine branches of the same nerve and the palatine artery which pass through the **posterior palatine foramen** of the maxilla and several

other small apertures in both the palatine and maxilla in its neighbourhood. A short way up the inner part of this main lateral plate is given off a horizontal lamina which passes inwards, coming in contact with the pre-sphenoid for a short distance and running forward along the vomer for some way. This lamina forms the dorso-lateral wall of the narial passage and separates it from the orbit. More ventrally the main lateral plate gives off another horizontal extension, the **palatal process,** which passes inwards and forwards to the level of the fourth pre-molar, to join with its fellow in the middle line and form, not only the ventral wall of the narial passage, but also the posterior portion of the hard bony roof of the mouth. The posterior nares therefore come to be bounded by the palatine bones save for a small part on their dorsal side which is filled in by the vomer.

The **maxillæ** are two large bones forming the major portion of the lateral walls of the nasal capsules. The main mass or body of the maxilla, termed the alveolar portion of the maxilla, completes the antero-ventral wall of the orbit. Right in the front corner it is perforated by the hinder opening of the **infra-orbital canal,** through which the infra-orbital branch of the trigeminal nerve passes to be distributed to the upper lip and vibrissæ. It makes its exit by the well-marked **infra-orbital foramen** just in front of and below the orbit. From the body of the maxilla a frontal wing passes upwards helping to form the roof of the nasal chamber and touching the pre-maxillæ, the nasal, the frontal and lachrymal bones. The body also gives off a palatine lamella which joins with its fellow in the mid-ventral line, constituting a large part of the hard palate. At its hinder edge this plate of bone joins the palatine in a curved suture running in a postero-lateral direction, and about half-way along this suture occurs the posterior palatine foramen which, as already noted, transmits the palatine nerves and arteries. The front end of the palatine plate touches the pre-maxillæ and forms the posterior walls of the anterior palatine foramina. The junction of the body of the maxilla and the palatine plate is termed the alveolar border, since in it lie the alveoli of the canine, premolar and molar teeth. From the postero-lateral border of the body of the maxilla a short pointed **zygomatic process** runs backwards, taking part in the formation of the zygomatic arch.

The **pre-maxillæ** are the most anterior of the bones of the skull, completing the front portion of the upper jaw, and they bear the alveoli of the incisor teeth. They are joined laterally to the maxillæ and in the middle line with one another, thus forming the lower and side borders of the anterior nares. Postero-dorsally each sends off a long narrow tongue, the **nasal process,** which lies between the nasal

bone and the maxilla on each side. They also give off ventrally a small palatine process in the middle line which form the mesial borders of the **anterior palatine foramina,** long oval apertures whose postero-lateral rims are completed by the maxillæ, through which pass the naso-palatine branches of the facial nerve.

The **malar or jugal bone** is a thin flat bone attached to the body of the maxilla near the zygomatic process. It runs out posteriorly, intimately connected with this process and unites with a similarly named projection from the squamosal bone. At its upper dorsal corner it bears a slight prominence, the **post-orbital process,** opposite to the similarly named structure on the frontal bone. These two processes are but little marked in *Canis*, but in other mammals they may be much more strongly developed and even join one another so that superficially, at any rate, the orbital and temporal fossæ are completely separated.

The **squamosal** bone is a broad scale-like bone at the lower hinder end of the temporal fossa. Posteriorly it is bounded by the ex-occipital and supra-occipital, above by the parietal, antero-ventrally by the alisphenoid, and the hinder part of its ventral border articulates with the tympanic bone. Immediately in front of the bulla it sends out a stout perpendicular process, the under surface of which is hollowed and smooth to form an articular surface, the **glenoid facet,** for the lower jaw. At the hinder edge of the facet is a projection running downwards, the **post-glenoid process,** perforated behind by the **post-glenoid foramen** for a branch of the lateral sinus. This outgrowth, the **zygomatic process,** then turns forwards and joins the jugal by a long oblique suture, thus completing the **zygoma** or zygomatic arch.

The **mandible,** or lower jaw, consists of two elongated somewhat triangular bony plates, the **rami,** compressed laterally, which unite in front by roughened surfaces, forming the **mandibular symphysis.** Their union is not complete save in quite old specimens, and they generally fall apart in prepared skeletons. The upper or alveolar border bears the teeth. At its postero-ventral extremity it juts out to form a well-marked projection, the **angular process.** Just above this and separated from it by a notch is a strong transverse ridge, the **condyle,** rounded in the antero-posterior direction and serving for articulation with the facet of the squamosal bone. From the structure of the condyle and the facet it is clear that the jaw is only capable of a simple up-and-down motion. Between the condyle and the last tooth the upper edge of the ramus is thrown up into a laterally compressed, backwardly curved wing, the **coronoid process.** Below this and in front of the condyle on the outer side of the jaw is a hollow space on to which the masseter muscle of

the mandible is inserted. On the inner side of the ramus just below and in front of the condyle lies the **inferior dental foramen,** which allows the inferior dental nerve, a branch of the trigeminal, and the similarly named artery that accompanies it to enter the substance of the bone. A terminal branch of the same nerve leaves the outer surface of the jaw by the **mental foramen,** just behind and below

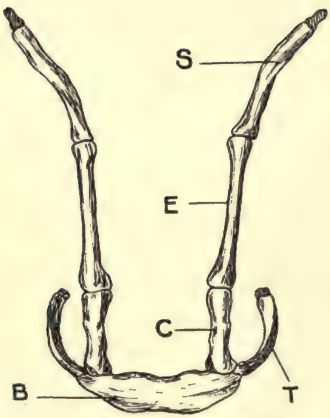


FIG. 101.—Hyoid bone of *Canis*.

B., body of hyoid, basi-hyal; C., cerato-hyal; E., epi-hyal; S., stylo-hyal; C+E+S=anterior; T., thyro-hyal, posterior cornu.

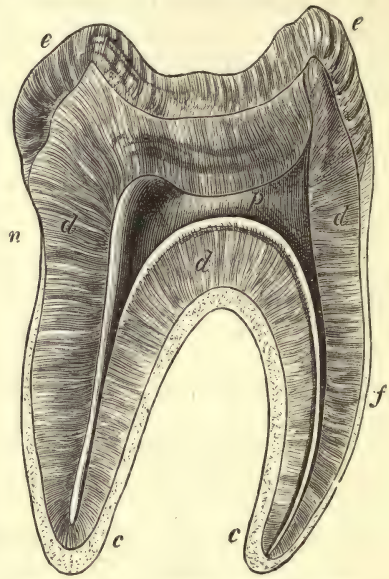


FIG. 102.—Longitudinal section of a molar tooth.—From Owen.

k., crown; *n.*, neck; *f.*, fangs; *e.*, enamel; *d.*, dentine; *c.*, cement; *p.*, pulp cavity.

the canine tooth, and is distributed to the lip and surrounding tissues.

The hyoidean apparatus is composed of a median portion, the **basi-hyal,** and a pair of anterior and a pair of posterior cornua. The basi-hyal, or body of the hyoid, is a small transverse flattened bar of cartilage bone somewhat thickened and turned up at its ends. The posterior cornua are short rods of bone articulating with the outer extremities of the basi-hyal. They pass upwards and are attached to the thyroid cartilage of the larynx and hence are termed the **thyro-hyals.** The anterior cornua are longer rods passing in a curved manner upwards and outwards and forming a connection with the cranium in the region of the tympanic bone. This ossifies in four parts; the most dorsal is the **tympano-hyal,** a

small bony mass lying in between the tympanic and peri-otic bones just in front of the stylomastoid foramen. It is hardly distinguishable in most dogs, though plain in some other mammals. The remaining portions of the cornua passing from dorsal to ventral end are the **stylo-hyal,** the **epi-hyal** and the **cerato-hyal,** which joins the body near the thyro-hyal.

A typical tooth consists of a **crown,** the portion standing out from the gum ; a **root,** which is inserted in the jaw and may possess one or more fangs ; and a slightly constricted region, the **neck,** joining the other two. Within the tooth is a hollow, the **pulp cavity,** containing the pulp, which is connective tissue richly supplied with blood-vessels and a nerve.

The main mass of the tooth is composed of the hard **dentine.** The crown is capped with a still harder substance, the **enamel,** and the fangs are coated with **cement.** This is a softer substance resembling bone, in that it possesses lacunæ and canaliculi, but it has no Haversian canals.

CHAPTER XII

LEPUS CUNICULUS—(*continued*)

Digestive System—Respiratory System—Circulatory System—The Mammalian Heart—Urogenital System—Ductless Glands.

Digestive System.

The digestive system is composed of the alimentary canal and its related glands, and in the rabbit consists of the same main parts as in *Rana*.

The mouth is bordered by very freely movable lips of which the upper, as has been noted, is cleft. The buccal cavity is narrow and long as compared with the frog. Within the jaws are the teeth whose form and distribution we have already considered. The roof of the buccal cavity is composed of a mass of tissue termed the **palate.** The nasal cavities, instead of communicating by the internal nares with the front end of the buccal cavity, pass into long passages, the **narial canals,** which open by the nares back in the pharyngeal region, and it is the palate that constitutes the partition separating the buccal cavity from these canals. The front part of this roof contains osseous structures, namely, the palatine processes of the pre-maxillæ, the maxillæ and the palatine bone; it is consequently termed the **hard palate.** The hinder part, on the contrary, is composed entirely of membrane and connective tissue and so is designated the **soft palate.** Right at the front end of the palate are a pair of grooves terminating in small apertures, just behind the posterior incisors, which lead into the **naso-palatine canals,** and these form a means of communication between the anterior portions of the nasal chambers and the buccal cavity. In the sides of the hinder end of the soft palate are two small pits, the **tonsils.** The floor of the mouth cavity is mainly occupied by the long prominent muscular tongue, which unlike that in *Rana* is attached posteriorly and free in front. It is covered with tiny white spots that mark the position of the **taste papillæ.** On the sides of the posterior end of the tongue, level with the last molar teeth, are a pair of oval patches crossed by parallel ridges and termed the **papillæ foliatæ.** Just above and

behind these are a pair of small white spots surrounded by shallow circular grooves and termed the **circumvallate papillæ.**

Opening into the buccal cavity by means of ducts are four pairs of **salivary glands** whose function is to produce the saliva—the action of which on the food has already been discussed in connection with digestion. The **infra-orbital glands** are fairly large irregularly lobate glands situated just below the eyeball. Their ducts pass downwards to open on the inside of the cheek nearly opposite to the second pre-molar tooth. The **parotid gland** is a soft mass on each side just below the skin and lying in front of and below the base of the external ear, between it and the mandible. Its duct, the **Stenonion duct,** passes close beneath the skin parallel with the zygomatic arch to open on the inside of the cheek near the preceding duct. The **sub-maxillary gland** is a compact, red, ovoidal structure situated just inside the angle of the mandible, and its canal, **Wharton's duct,** runs along the inner side of the lower jaw to open midway between the posterior incisors and the base of the tongue. The fourth pair are the **sub-lingual glands,** elongated flattened red bodies situated on the inner side of the ramus, between it and Wharton's duct, near the openings of which their own ducts terminate.

The **organs of Jacobson** are two small tubular bodies embedded in the front end of the hard palate just above the palatine processes of the pre-maxillæ. They communicate with the nostrils in front and by means of the naso-palatine canals with the buccal cavity. Their functional significance is not apparent.

The buccal cavity passes backwards into the pharynx and the point of transition is marked dorsally by the termination of the soft palate, so that the posterior nares or ends of the narial passages also lead into it, uniting to form one **posterior nasal chamber** just before so doing. Into this chamber open the **Eustachian tubes** leading from the tympanic cavities of the ears. On the floor of the pharynx is a fairly large opening, the **glottis,** leading into the **larynx** and so allowing air to reach the lungs. From the front wall of this opening, a thin bilobed flap of cartilage, the **epiglottis,** projects upwards into the pharynx. In swallowing, this flap is bent down and so closes the glottis, preventing the entry of food. The pharynx continues on into the œsophagus. It will be seen then, that the Eustachian tubes, internal nares and laryngeal opening are all in close proximity in *Lepus*, and this is the case in mammals generally, hence certain diseases are liable to affect ear, nose and throat at the same time.

The œsophagus is a narrow dilatable tube running along the neck and through the thoracic cavity close below the vertebral

column, to pass through the diaphragm. A short distance inside the abdominal cavity it opens by an aperture termed the **cardia** into the stomach on the left side of its anterior wall. Its walls are fairly thick, containing non-striate muscle fibres and it is lined by a mucous membrane. The stomach itself is a wide dilated sac-like structure, rounded and much larger at the left or **cardiac end** and narrower and smaller at the right or **pyloric end.** It is asymmetrically situated, its main mass lying to the left of the middle line. It terminates on the right in a constriction, the **pylorus,** where it is narrowed down to a small opening leading on into the intestine. This passage is guarded by a ridge of the mucous membrane and a circle of muscles, constituting the **pyloric sphincter,** which enables the stomach to be shut off from the intestine during the preliminary stages of digestion. By means of its muscle layers the stomach is able to keep the food in it churned up until it is ready to be passed on. The first part of the intestine is the **duodenum,** and this takes the form of a long U-shaped loop, held together by an omentum and running almost the whole length of the abdominal cavity on the right side.

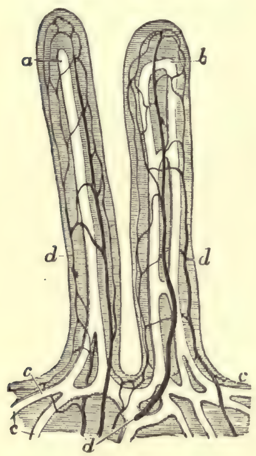


FIG. 103.—Two intestinal villi. Magnified 100 diameters.—From Quain.

a., *b.*, and *c.*, lacteals ; *d.*, blood-vessels.

The duodenum passes on into a very similar shaped tube, the small intestine or **ileum,** about seven or eight feet long, and thrown into a series of folds held together by omenta. On its walls appear, here and there, small granular areas slightly darker in colour than the remainder. These are known as **Peyer's patches,** and while, like the tonsils, they consist of lymphoid nodules, their exact significance has not yet been ascertained. The walls of the small intestine will be found to be thrown up into a number of small, closely set, blunt papillæ the **villi,** giving it the appearance of the "pile" of a carpet. Each is supplied with blood-vessels and also lymphatics, and by their means a large part of the absorption is carried on ; the blood-vessels taking up the soluble food and the lymphatics the emulsified fat. The ileum terminates in a swollen portion, the **sacculus rotundus,** whose walls are similar in structure to the patches, and this opens into the next part of the intestine a short distance beyond the proximal end of the latter. This part of the gut, the large intestine or **colon,** is about one and a half feet long, and

noticeably wider than the preceding portions. Its walls are pursed up into a series of marked sacculations, arranged at first in three longitudinal rows, then in two rows, then in one and finally disappearing altogether and leaving its wall smooth. This then passes over into the terminal portion of the gut, the **rectum,** a tube about two and a half feet long, about the same diameter as the small intestine ; it is slightly bent at first, but finally runs straight backwards through the pelvic cavity to open externally at the anus. Throughout its length it is usually marked by the presence of a series of pill-shaped bodies, the **fæces.**

At the junction of the ileum and colon is a large blindly ending tube, the **cœcum,** which is not represented in the frog or dogfish. It is a little longer and much wider than the colon and its greenish coloured, thin walls exhibit about twenty-five turns of a spiral constriction. Proximally it opens into the colon and distally it ends in a narrower thick-walled **vermiform appendix,** about four inches long, whose walls are granular in texture and pinkish in colour. Animals confined to a vegetable diet, *i.e.* herbivores, have a more specialised alimentary canal than carnivorous animals, and we find that they possess either a complicated stomach composed of several chambers, or if the stomach be simple as in *Lepus* there is present a large cœcum.

The digestive glands comprise, in addition to those in the walls of the stomach and intestine, the liver and pancreas.

The liver is a large brown five-lobed mass lying anterior to the stomach with its front surface curved convexly to fit on to the diaphragm, and its hinder surface hollowed out for the various parts of the stomach. It is attached to the dorsal body wall by a fold of mesentery, and also to the diaphragm by a vertical fold of peritoneum, the **suspensory ligament,** which also marks the division of the gland into right and left halves. The two median lobes, one on each side of the ligament, are termed the **right** and **left central lobes** respectively. Outside the left central lobe and between it and the cardiac end of the stomach lies the **left lateral lobe.** Externally to the right central lobe is the **caudate lobe,** which is applied to the anterior surface of the pyloric end of the stomach and postero-dorsally is hollowed to fit over the front end of the right kidney. The remaining lobe, the **Spigelian,** is shaped so as to fit closely against the median antero-dorsal surface of the stomach. The gall-bladder is a longish thin-walled sac partially embedded in the ventro-median border of the right central lobe, and from it a duct about two inches long passes backwards to open into the duodenum just a short distance beyond the pylorus. From each lobe of the liver comes a **hepatic duct** to open into this main duct

in which therefore two portions can be distinguished, a **cystic duct** coming from the bladder, and a **common bile duct** after the various hepatic ducts have joined it.

The pancreas in *Lepus* is unlike that in *Scyllium* or *Rana*, in that it does not form one discrete solid mass. On the contrary it takes the form of a number of scattered glandular nodules generally distributed throughout the omentum of the duodenal loop. They appear almost like little lumps of fat slightly tinged with pink and are more closely aggregated towards the anterior end. Here the pancreatic duct starts and thence runs backwards, receiving small ducts from the various nodules to open into the distal loop of the duodenum about three inches beyond the bend.

While not actually forming part of the alimentary system we find, as in the dogfish and frog, the spleen closely attached to the stomach by a **gastro-splenic omentum.** It has the form of an elongated strip of tissue of dark red colour lying in the cardiac region of the stomach.

A general outline of the digestive processes in a vertebrate and the parts played therein by the various parts of the alimentary canal have already been considered when dealing with the frog, so that it is not necessary to repeat them again here.

Respiratory System.

As pointed out already the glottis, protected by the epiglottis, lies on the floor of the pharynx ; it leads into a cavity, the **larynx,** or organ of voice. The wall of the hollow is supported by cartilages of which the first is termed the **thyroid,** and this takes the form of a wide band incomplete dorsally. The second cartilage is the **cricoid** which forms a complete loop, narrow ventrally and broad dorsally. Articulating with the antero-dorsal edge of the cricoid is a pair of small cartilages, the **arytenoids.** Stretching across the laryngeal cavity dorso-ventrally are a pair of membranous flaps strengthened by fibro-elastic ligaments ; these are termed the **vocal cords,** since their vibrations produce the voice. They are attached ventrally to the thyroid and dorsally to the cricoid cartilages. The presence of a fairly long neck makes it impossible for the larynx to lead directly into the lungs as in *Rana*, and consequently we find a longish straight tube, the **trachea** or wind-pipe, connecting the two. The trachea lies on the ventral side of the œsophagus between it and the skin of the neck. Throughout the whole of its length it is strengthened by a series of cartilaginous rings incomplete dorsally, which keep it open and nevertheless allow for a certain amount of distention of the adjacent œsophagus. It enters the thoracic cavity and passes dorsal to the

heart about half-way along which it divides into two branches, the **bronchi,** one going to each lung. These divide up into smaller and smaller tubes, the **bronchioles,** also supported by small cartilaginous rings, thus constituting a system of vessels through which the air is conveyed to all parts of the lungs. The lungs themselves are soft spongy pink bodies, and not hollowed sacs as in *Rana*, lying freely in the thoracic cavity unattached save where the bronchi and blood-vessels enter them. Each is divided into two main lobes, but there are on the right side two small accessory lobes of which the posterior and smallest lies in the middle line closely applied to the œsophagus just behind the heart. The ultimate branches of the bronchioles finally open into saccular chambers, the **alveoli,** where the actual respiratory exchanges take place.

The peritoneum lines the thoracic cavity and is reflected round each lung separately and is termed the **pleura,** being divided into the parietal pleura lining the wall of the cavity and the visceral pleura around the lungs. Thus we can see that each lung has its own pleural cavity, and further the two lungs are separated in the middle line by the two layers of the pleura, constituting the mediastinum and enclosing between them the mediastinal space. Within this lie the œsophagus, heart, main blood-vessels, the end of the trachea and the beginnings of the bronchi, and the space is shaped so as to accommodate them.

The mechanism of breathing differs much from that in the frog owing to the presence of the ribs and sternum making an airtight compartment for the lungs. The ribs lie somewhat obliquely and by means of the intercostal muscles they can be raised in such a manner as to enlarge the thoracic cavity, and the relaxation of these muscles allows the chest to return to its original size. This operation brings about what is termed **costal breathing**. Further, the floor of the cavity is formed by the arched diaphragm which, when its muscles contract, flattens, and so increases the capacity of the thorax, the return is accomplished by the relaxing of these muscles again and this brings about **diaphragmal breathing**. In normal respiration both types play their part, and so air is drawn into the lungs by the enlargement of the cavity. Their emptying is brought about in part by the elasticity of the lungs themselves, but also by a return to their original positions of the ribs and diaphragm.

Circulatory System.

The circulatory system consists of the same main divisions as in the frog, but it differs considerably in points of detail and represents a higher stage of development.

The centre of the system is the heart, and while the heart of the rabbit is typically mammalian, yet owing to its small size it is not easy to examine, and after considering the rest of the circulatory system we shall return to consider a mammalian heart as exemplified in a larger animal such as the pig or sheep. It is sufficient to note only the main points here. The heart consists of four chambers, two **atria** with **auricular appendages** and two ventricles, a right and a left in each case, and the cavities of one side of the heart have no means of communicating directly with those of the other. Into these chambers open or from them come off the main vessels, there being no structures corresponding with the sinus venosus or conus arteriosus of *Rana*.

Arterial System.

The arterial system is divided into two portions, the pulmonary and the systemic. The **pulmonary artery** takes origin from the antero-median corner of the right ventricle, passes forwards and arches over to the dorsal side of the left atrium where it divides into two branches, one going to each lung. The base of the pulmonary artery is guarded by three tough membranous pocket-shaped **semilunar valves.**

The systemic arteries are all served by a single large trunk, the **aorta** or **aortic arch,** which arises from the left ventricle and, passing forwards dorsal to the pulmonary artery arches, over the atrium, and the left bronchus reaches the left side of the vertebral column along which it runs backwards as the **dorsal aorta.** Upon entering the abdomen it takes up a median position below the centra. Just before the pulmonary artery divides into two it is joined to the aorta by a band of fibrous tissue, the **ligamentum arteriosum,** which in the embryo is an open tube, the **ductus arteriosus,** and is the remnant of the connection between these vessels in the embryo and also in the primitive vertebrate, just as the ligamentum caroticum of *Rana* is the persistent remains of another of these connections. The base of the aorta is guarded by a series of three pocket-shaped **semilunar valves,** similar to those in the pulmonary artery, which prevent the blood passing back again into the ventricle. Behind two of these valves are the openings of two small **coronary arteries** which carry blood to the tissues of the heart itself. Just at the point where the aorta is arching over it gives rise to a short stout **innominate artery,** turning off to the right side, which after a short course divides into the **right common carotid** and **right subclavian arteries.** The right common carotid artery runs forward alongside the trachea, giving off branches to it and other tissues of the neck up to the level of the angle of the jaw. Here it divides

into the **internal carotid,** which enters the cranium through the carotid foramen and is distributed to the brain, and the **external carotid,** which ramifies over the whole of the right side of the face and head. The right sub-clavian passes straight outwards towards the right fore limb. A short distance along this artery is given off a small **vertebral artery.** This runs forwards and inwards to pass into the vertebrarterial canal supplying the spinal cord and also the posterior end of the brain. A little way further on arises an **intercostal artery** which, passing backwards, gives off side branches to the first few intercostal spaces. Right close to it arises another small artery, the **anterior epigastric** (internal mammary), which runs laterally down the inside of the ventral thoracic wall. The sub-clavian then gives off certain branches to the shoulder girdle and axillary region, and as the **brachial artery** goes on into the arm which it supplies.

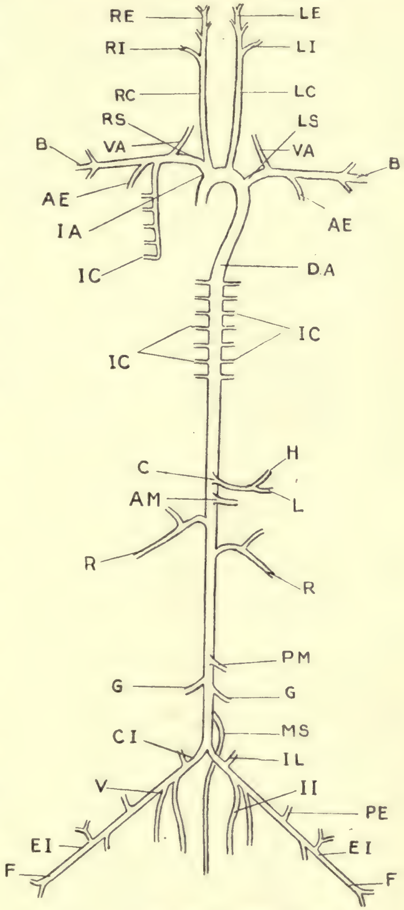


FIG. 104.—Diagram of the arterial system of *Lepus*.

A.E., anterior epigastric; A.M., anterior mesenteric; B., brachial; C., cœliac; C.I., common iliac; D.A., dorsal aorta; E.I., external iliac; F., femoral; G., genital; H., hepatic; I.A. innominate; I.C., intercostal; I.I., internal iliac; I.L., ilio-lumbar; L., lieno-gastric; L.C., left common carotid; L.E., left external carotid; L.I., left internal carotid; L.S., left sub-clavian; M.S., median sacral; P.E., posterior epigastric; P.M., posterior mesenteric; R., renal; R.C., right common carotid; R.E., right external carotid; R. I., right internal carotid; R.S., right sub-clavian; V., vesicular; V.A., vertebral.

A short distance further along the main aortic arch gives rise to the **left common carotid artery,** which passes up the trachea and is distributed in a similar manner to the right. Beyond this again, as the aorta reaches the vertebral column it gives off the **left sub-clavian artery,** which runs outwards to become the brachial after giving

off the same branches as the right with the exception of the intercostal.

The aorta then runs on giving off a short series of paired **intercostal arteries** to the posterior intercostal spaces, and then some distance behind the diaphragm gives off a large median **cœliac artery** which, after a short course in the mesentery, divides into a hepatic trunk going to the liver and a **lieno-gastric** branch supplying the stomach and spleen. A second large artery, the **anterior mesenteric,** arises just posterior to the foregoing and divides up to go to the duodenum, pancreas, small intestine, cœcum and colon. This is followed by a pair of **renal arteries** which, after giving off a branch to the musculature of the dorsal body wall, proceeds to the kidney. The right vessel arises a short distance ahead of the left. Some distance further back arise a similar asymmetrical pair of **genital arteries** differently named in the two sexes. In the female the **ovarian arteries** pass out laterally to the ovaries, but in the male, owing to the migration of the testes, the **spermatic arteries** run outwards for a short distance and then back and into the scrotal sacs. The **posterior mesenteric artery** is a small median vessel originating just before or just behind the genitals and going to the hinder part of the rectum. Posterior to this the **median sacral artery** is given off from the dorsal side of the aorta and it runs parallel with this to the tail: it is probably to be regarded as being actually the continuation of the aorta itself. Shortly after this the main vessel—the so-called aorta—bifurcates to form the **common iliac arteries,** which pass out at an angle laterally towards the legs. A short way along each vessel gives off on its anterior side an **ilio-lumbar artery** to the dorsal body wall. This is followed by a pair of arteries, the **internal iliac** and the **vesicular,** on the posterior wall. The former spreads over the dorsal wall of the pelvic cavity and the latter supplies the bladder. Another small artery, the **posterior epigastric,** is given off from the anterior wall of the main trunk which may now be termed the **external iliac**. It passes up the ventral abdominal wall. Finally the external iliac passes on into the leg as the **femoral artery.**

Venous System.

The veins of the body can be considered as falling into three more or less independent, but nevertheless related groups of vessels and dealt with under the headings: the pulmonary system, the hepatic portal system and the system of the caval veins.

The **pulmonary veins** bring the blood back from the lungs. Each one is formed by the union of two main trunks coming from those bodies quite close to the heart and they open into the right atrium.

The **hepatic portal system** consists of a series of veins coming from all parts of the alimentary canal which ultimately unite to form a large vessel, the **hepatic portal vein,** which, passing forward in the mesentery near the post-caval vein, divides into branches going to the various lobes of the liver. Its various factors can readily be made out in a freshly killed animal when they are usually full of blood. Four main trunks can be readily distinguished. The **posterior mesenteric vein** comes from the hinder portion of the rectum, and lies mainly in the mesorectum. The **anterior mesenteric vein** is a larger trunk formed by the union of numerous vessels coming from the front part of the rectum, the ilium, the coccum and the colon. The duodenal loop and the pancreas are drained by a single vessel, the **duodenal vein,** and the blood from the stomach and spleen is returned by a **lieno-gastric vein.**

Three main systemic or caval veins are present, two anterior and one posterior. The **right pre-caval vein** (**vena cava anterior dextra**) is formed by the junction of the jugular and sub-clavian veins just in front of the first rib. It runs back on the inner side of the right lung, and opens into the dorsal wall of the right atrium. The **azygos vein** (**azygos cardinal**) is a small vessel running forward along the right side of the vertebral column from the posterior end of the thorax, receiving, as it does so, factors from the hinder intercostal spaces. Finally it passes round the œsophagus to open into the pre-caval, just before this enters the atrium. In spite of its small size it is of interest, since it represents the persistent remnant of the right posterior cardinal vein of the lower vertebrates such as the dogfish, while all trace of it has disappeared in the frog. The **anterior phrenic vein** is a small vessel bringing blood from the ventral portion of the diaphragm, and opening into the ventral side of the pre-caval. The **right anterior intercostal vein** is a short dorsally situated vessel receiving factors from the anterior four or five intercostal spaces and opening close to the preceding vein. The **right anterior epigastric vein** (internal mammary) lies on the ventral thoracic wall in close proximity to the corresponding artery, and it joins the caval vein at the level of the first rib.

The **right sub-clavian vein** is a stout trunk which drains the right fore limbs and shoulder girdle, being termed the **brachial vein,** in the upper arm.

The **right external jugular** is a large vein running fairly superficially the whole length of the neck, from just behind the angle of the jaw where it is formed by the confluence of the **anterior** and **posterior facial veins,** to the point where it joins the sub-clavian. It drains the whole of the facial region and receives factors from the œsophagus, trachea and various tissues of the neck. It has

previously been pointed out that the **internal jugular vein** leaves the cranial cavity through the foramen lacerum posterius in company with the ninth, tenth and eleventh cranial nerves. From this point it runs back along the side of the trachea to enter the external jugular vein just before this joins the sub-clavian, and the trunk formed by the union of these two vessels is sometimes designated the **common jugular vein.**

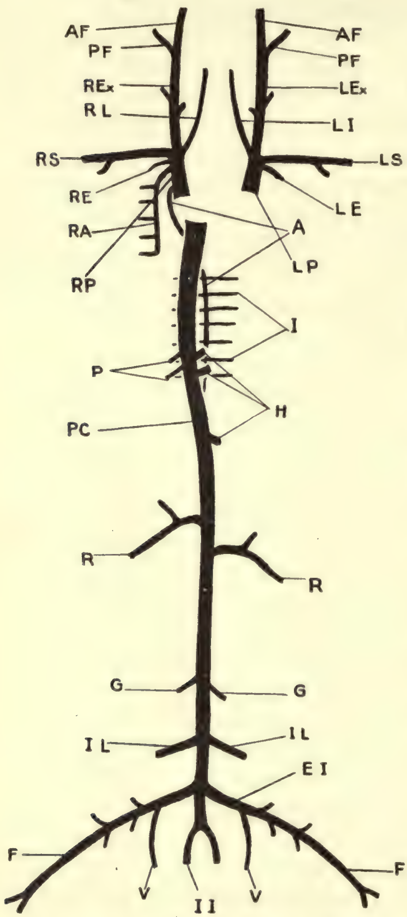


FIG. 105.—Diagram of the venous system of *Lepus*.

A., azygos; A.F., anterior facial; E.I., external iliac; F., femoral; G., genital; H., hepatic; I., intercostals; I.I., internal iliac; I.L., ilio-lumbar; L.E., left anterior epigastric; L.Ex., left external jugular; L.I., left internal jugular; L.P., left pre-caval; L.S., left sub-clavian; P., phrenics; P.C., post-caval; P.F., posterior facial; R., renal; R.A., right anterior intercostal; R.E., right anterior epigastric; R.Ex., right external jugular; R.I., right internal jugular; R.P., right pre-caval; R.S., right sub-clavian; V., vesicular.

The **left pre-caval vein (vena cava anterior sinistra) is** constituted in a similar way to the right, with the one important exception that it receives no azygos vein. After its formation in front of the first rib it enters the thoracic cavity, passes back along the inner side of the left lung and crosses between the heart and the root of the left lung to enter the left dorsal wall of the right atrium.

The **post-caval vein (vena cava posterior)** is a large trunk formed at the posterior end of the abdominal cavity by the union of the two internal iliac veins. Thence it runs forward beneath the vertebral column slightly to one side of and close to the aorta up to the liver, in the dorsal surface of which it becomes embedded. It enters the thorax through an aperture in the central tendon of the diaphragm, and runs forward slightly to the right of the middle

line and opens into the postero-dorsal wall of the right atrium. The **internal iliac veins** drain the back of the thighs, and run in the dorsal wall of the pelvic cavity, at the anterior end of which they unite to form the post-caval. A short distance in front of this the two **external iliacs** enter the main trunk. They are large vessels coming from the hind limb along the pre-axial side of which they run as the **femoral veins.** In the abdominal cavity they receive small veins, including a **vesicular,** from the urinary bladder, and in the female rabbit also branches from the uterus. Just in front of this again the post-caval receives the paired **ilio-lumbar veins,** which bring blood back from the posterior abdominal walls. Still more anteriorly are the **genital veins,** the **spermatic veins** in the male and **ovarian veins** in the female. In the female they pass practically straight outwards, but in the male they pass outwards a short way and then backwards in company with the corresponding artery into the scrotal sacs. The **renal veins** which open more anteriorly, although paired, are asymmetrical, the right being shorter, about three-quarters of an inch long and in front of the left. A certain amount of variation is to be found in the veins of the posterior end of the abdomen, for the left spermatic vein sometimes enters the ilio-lumbar or the renal of the same side instead of entering the post-caval separately. Large **hepatic veins** return blood from the various lobes of the liver, and enter the post-caval as it passes through this gland. As a rule about four large trunks can be distinguished coming from the liver. The diaphragm is drained by the small **phrenic veins** running in its substance, the most ventral of these open into the pre-caval veins, but the others flow into the post-caval as it passes through the central tendon.

It will be noticed that there is a much closer correspondence between the arteries and veins in *Lepus* than in *Rana*, and indeed over the greater part of the system we find that the main vessels of the two systems accompany one another.

Attention has already been called to the fact that the heart is a very important organ, but as it has only been dealt with in broad outline, we may return to the question here.

Mammalian Heart.

The heart of the mammal is an important organ, and as it is so small in the rabbit it is advisable to study its structure in a larger animal such as the pig or the sheep. It should be borne in mind that there are slight differences in the relationship of the main veins to the atria and the main branches of the arteries in the three types. They are only of minor importance, however, and do not affect the general plan, so that they need not be considered here.

In making a practical examination of a heart care should be taken to choose a specimen that has not been damaged in removal from the body, and one that has the bases of the main arteries and veins left as long as possible. If a sheep's heart be chosen, it is often advisable to remove the greater part of the fat attached to it before starting dissection. The following description is based mainly on the heart of the sheep.

The mammalian heart is a somewhat conical structure lying almost in the mid-ventral line of the thorax with its broader end, the **basis cordis** or base, directed anteriorly and to the right, and the

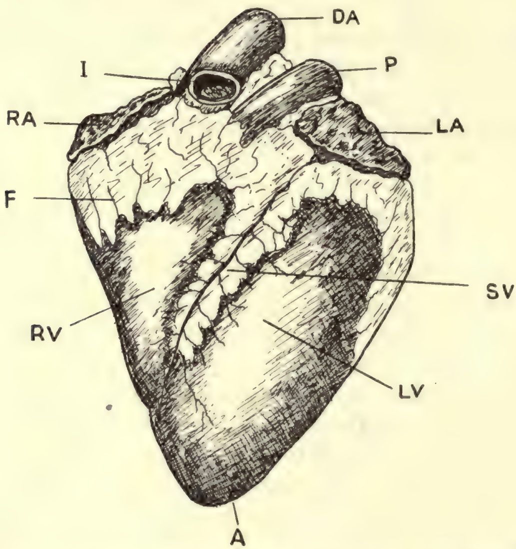


FIG. 106.—Ventral view of sheep's heart with atria collapsed.

A., apex ; D.A., dorsal aorta ; F., fatty tissue ; I., innominate artery ; L.A., left auricle ; L.V., left ventricle ; P., pulmonary artery ; R.A., right auricle ; R.V., right ventricle ; S.V., sinus longitudinalis ventralis.

bluntly-pointed **apex cordis** pointing posteriorly and to the left. It consists of four entirely separate chambers, a right and left ventricle and a right and left atrium, and when empty the main part of its bulk consists of the two large fleshy ventricles with parts of the atria appearing as flaps upon them, and separated by the deep **coronary sulcus.** In the body the heart is enclosed in a double-walled sac, the **pericardium,** whose inner layer is tightly attached to the wall of the heart, and whose loose outer layer is generally removed in taking the heart from the body. The line where the inner layer is reflected to form the outer will be seen

in the atrial region around the bases of the main blood-vessels. Between the two layers is the **pericardial space,** filled in life with a lymph-like pericardial fluid.

On the ventral, more rounded surface of the heart a shallow groove containing small blood-vessels, the **sulcus longitudinalis ventralis,** runs from a point on the base to the left of the middle line obliquely across to the right side, a short distance above the apex. A somewhat similar but shallower groove also containing blood-vessels, the **sulcus longitudinalis dorsalis,** is present on the dorsal, flatter

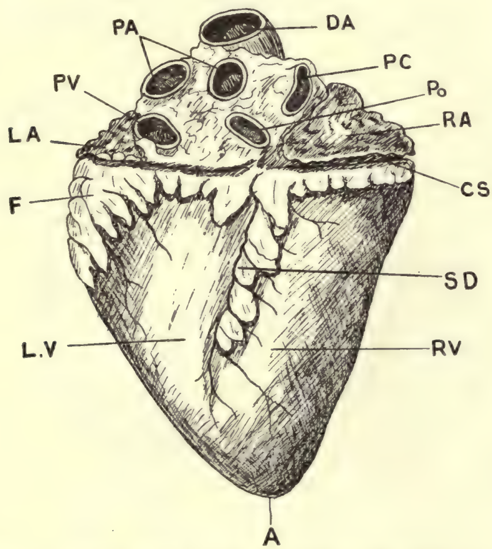


FIG. 107.—Dorsal view of sheep's heart with atria collapsed.

A., apex ; C.S., coronary sulcus ; D.A., dorsal aorta ; F., fatty tissue ; L.A., left auricle ; L.V., left ventricle ; P.A., pulmonary arteries ; P.C., pre-caval veins ; Po., post-caval veins ; P.V., pulmonary vein ; R.A., right auricle ; R.V., right ventricle ; S.D., sinus longitudinalis dorsalis.

side of the heart. These two external grooves mark the position of an internal partition separating right and left ventricles. The atria are marked off from the ventricles by a very deep cleft, the **coronary sulcus,** that runs completely round the heart save where it is interrupted by the main blood-vessels.

The two atria when inflated appear on the external dorsal surface almost as one large thin-walled sac, but they are nevertheless completely separated internally by the **septum atriorum.** Each atrium consists of a hollow sac with a thin wall, and bears at its outer corner a thicker appendage, the **auricle,** internally marked by a

series of interlacing muscular ridges, the **musculi pectinati**. It is these appendages that show prominently externally when the atria are deflated.

Into the right atrium open two large veins, the anterior and posterior caval veins, whose openings are separated by a ridge, the **tuberculum intervenosum,** and a smaller vessel, the coronany vein, bringing back the blood from the heart itself. A sinus venosus, such as we find in the frog, is not present, it having been absorbed into the atrium in the course of the evolution of the mammal. Into the left atrium open the two pulmonary veins. The septum atriorum is a fairly thin smooth-walled partition that completely separates the two atrial cavities, and in it is an oval area much

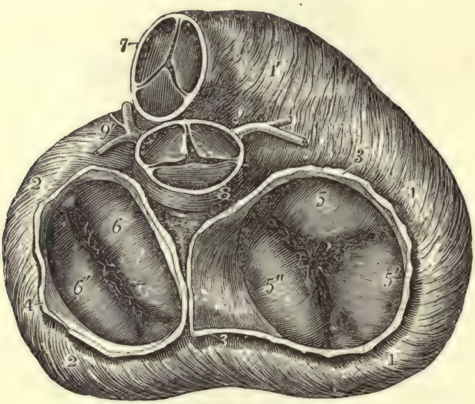


FIG. 108.—The base of the heart.—From Quain.

The auricles have been cut away, and the valves are closed. The pericardium has also been removed to expose the muscular fibres.

1 and 1′, right ventricle ; 2, left ventricle ; 3, wall of right auricle ; 4, wall of left auricle ; 5, 5′, and 5″, the tricuspid valve ; 6 and 6′, the mitral valve ; 7, pulmonary artery ; 8, aorta ; 9 and 9′, coronary arteries.

thinner than the rest and semi-transparent. This is termed the **fossa ovalis,** and in the embryo it was an aperture, leading directly from one cavity to the other. Each atrium opens into its corresponding ventricle by an **atrio-ventricular orifice** guarded by strong valves. On the right the valve is composed of three large, tough, membranous flaps, and so is termed the **tricuspid** valve, while on the left there are but two similar flaps constituting the **bicuspid** or **mitral valve**, from its somewhat fanciful resemblance to a bishop's mitre.

The ventricles stand in marked contrast with the auricles on account of their very thick, strongly muscular walls. Their cavities are completely separated by the **septum ventriculorum,** which is also thick and muscular. A transverse section through the

ventricular region shows a noticeable difference between the two sides. The cavity of the left ventricle appears almost circular in outline, and its walls are noticeably thicker than the right. The cavity of the right ventricle appears crescent-shaped and partly wrapped around the left, so that the latter ventricle with the septum ventriculorum occupies by far the larger part of the heart. The walls of both ventricles are seen to be thrown up internally into a series of prominent rounded muscular ridges, the **trabeculæ carneæ.** In order to strengthen them the edges of the atrio-ventricular valves are each provided with a number of tough ligamentous cords, the **chordæ tendineæ,** which take their origin from raised pyramidal muscular projections, the **musculi papillares,** on the walls of the ventricles.

From the anterior median end of the left ventricle comes off the large aorta, the main artery of the body, and at its base lie a series of three pocket-shaped **semilunar valves**, which can close it completely. Behind two of the valves are small apertures leading to the two coronary arteries, which supply the actual tissue of the heart itself. The large pulmonary artery originates from the anterior median end of the right ventricle, and this, too, is guarded at its base by three **semilunar valves** similar to those in the aorta. The pulmonary artery soon divides into two main branches, one going to each lung. The conus arteriosus no longer exists a separate element in the mammalian heart, it has been absorbed into the ventricle.

We may now consider quite briefly the action of the heart. Blood from the body is brought back by the Venæ cavæ into the right atrium, which, therefore, contains non-aerated blood. This is then passed into the right ventricle, and it leaves this through the pulmonary artery, so that, as there is no communication between one side of the heart and the other, the right side of the heart and all the vessels connected with it contain nothing but non-aerated blood. In the lungs the blood is aerated and brought back by the pulmonary veins to the left atrium, whence it passes to the left ventricle, and thence via the aorta to all parts of the body. The left side of the heart and its vessels, therefore, contain only aerated blood. We see then that in the vertebrate series we have three possible arrangements in the blood circulatory system. Firstly, in the fish, as exemplified by *Scyllium*, the blood goes from the single ventricle to the gills to be oxygenated, thence to the whole of the body, and finally back to the single atrium, by the ductus Cuvieri ; no other course is possible. This is then fitly termed a **single** or a **branchial circulation.** Secondly, in the mammal, as we have seen, blood from the body is brought to the right side of the

heart, taken thence to the lungs, back again to the left side of the heart, and thence to the body. Here, again, there is no alternative course ; to reach the same point again any given portion of blood must return twice to the heart, it must pass through both the pulmonary and systemic circulations. Such a condition we characterise as a **complete double circulation.** Lastly, in *Rana*, we have a condition in some respects intermediate between these two. While we have both a pulmonary and a systemic circulation, each related to a separate atrium, yet there is a possibility of a mixture of blood in either the ventricle or the conus arteriosus. It is conceivable, therefore, that any given portion of blood might only go to the heart once before returning again to the same point. We indicate this by describing the blood circulatory system of the frog as **incompletely double.**

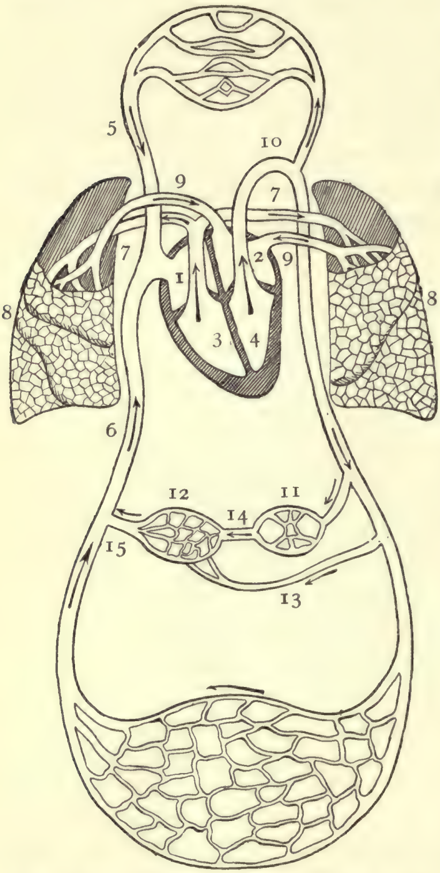


FIG. 109.—Diagram illustrating the circulation.—From Furneaux.

1, right atrium ; 2, left atrium ; 3, right ventricle ; 4, left ventricle ; 5, vena cava superior ; 6, vena cava inferior ; 7, pulmonary arteries ; 8, lungs ; 9, pulmonary veins ; 10, aorta ; 11, alimentary canal ; 12, liver ; 13, hepatic artery ; 14, portal vein ; 15, hepatic vein.

As in all land-dwelling vertebrates the blood in a mammal is kept circulatory through the lungs and the body by means of the alternate contraction and expansion, the two conditions passed through being termed **systole** and **diastole** respectively. The former commences practically simultaneously in the two atria, and drives the blood from these chambers into the ventricles. When these latter are filled and the pressure in them exceeds that in the atria, the blood attempts to flow back, but is prevented by the closure of the

atrio-ventricular valves. Following the sharp systole the atria pass through a relatively long period of slow distension or diastole. This period can only be considered long when compared with the time occupied by systole ; actually, of course, the whole time occupied by the two is measured in fractions of a second. In a similar manner the ventricle undergoes a sharp systole followed by a longer diastole, and naturally the end of ventricular diastole coincides with atrial systole. The atrial diastole, however, is not similarly related to ventricular systole, and there is a period of time when all chambers of the heart are in diastole. The contraction of the ventricles expels the blood through the aorta and pulmonary artery. These vessels having elastic walls enlarge with the inflow of blood, and as soon as the ventricular contraction relax, their elasticity tends to drive the blood back into the ventricle, a proceeding that is stopped by the rapid closure of the semilunar valves. It will be recalled that behind two of the aortic valves lie the apertures of the coronary arteries, and the blood is driven into the coronary circulation by this same reverse wave of pressure that shuts the valves. The elasticity of the walls of the two main arteries is sufficient to drive the blood onwards to the body or lungs as the case may be.

In listening to the heart beating within the thorax two distinct sounds can readily be made out. The first is a low, dull sound, and the second a higher, sharper one. The latter is found to be due to the closure of the semilunar valves at the bases of the two arterial trunks, while the former is the result of several causes, the principal among which are the tensing of the mass of the ventricular muscles, marking the beginning of systole and the practically simultaneous closure of the atrio-ventricular valves. It should be obvious then that imperfect structure or functioning of either sets of valves will affect the quality of the corresponding heart sound, and so can be detected by listening to the beat and comparing its sound with those made by the normal heart.

Urogenital System.

As in the frog we find that the excretory and reproductive systems are closely related anatomically, and while the sperms do not actually utilise the kidney ducts, the ends of the reproductive and excretory ducts are closely related in the two sexes, and the same external aperture serves for the emission of the urine and the genital products. This external opening is independent of the opening of the alimentary canal, and as it is concerned with the reproductive functions it naturally differs considerably in the two sexes.

The **kidneys** in the male lie in the abdominal cavity attached to the latero-dorsal wall of the cœlom, and as has been noticed in dealing with their vascular supply, the right kidney lies somewhat in front of the left. Each kidney is a flattened ovoidal body of dark red colour with a distinct notch, the **hilus,** on its inner surface marking the point at which the blood-vessels join it and the ureter leaves it. On cutting off the ventral half of the kidney it will be seen that the substance of which it is composed is distinguishable into two portions. The outer part, or **cortex,** is somewhat granular in appearance and marked by a series of small spots ; it is composed mainly of the much looped and twisted secretory portions of the uriniferous tubules, and the spots indicate the positions of the **Malpighian bodies.** The inner part, or **medulla,** is seen to be striated and it consists almost entirely of the collecting parts of the tubules which are nearly straight and cut lengthwise. It is drawn up into a pointed pyramidal projection, termed the **pyramid,** upon the blunt apex of which the tubules open. Inside the hilus is a crescentic cavity, the **pelvis** of the kidney, which represents the dilated extremity of the ureter, and lies within the body of the gland. The **ureters** are long, fairly narrow tubes passing along the dorsal body wall to enter directly into the bladder at the level of the front end of the pelvic symphysis. The **urinary bladder** itself is a large dilatable, muscular, thin-walled sac in which the urine is stored as it is secreted, and can be emptied at the will of the animal. The path from the bladder will be considered when treating of the reproductive organs, but it should be noted in passing that the ureters in *Lepus* open directly into the bladder, and not into the cloaca as in *Rana*. We find in the embryo, however, that they originally open into the dorsal wall of the rectum, from the opposite side of which is given off the ventral outgrowth destined to become the bladder. In the course of development, however, as the urogenital opening becomes separated from the end of the alimentary canal, the openings gradually migrate round the rectum until they pass on to the dorsal wall of the bladder itself.

During the embryonic history of the excretory organs two other kidneys make their appearance ; the first is the **pronephros,** and the second is the **mesonephros** or **Wolffian body,** but both of these disappear save for certain remnants which, however, lose their excreting function and become related to the reproductive organs. The functional kidney in the adult is the third to appear, and it is termed the **metanephros.** It differs from those preceding it in that its tubules are never segmentally arranged, but all open together at one point ; consequent upon this we find that from the very beginning its tubules are not related to the posterior segments of the

body, but it is a compact discrete organ. Then, too, the tubules do not possess nephrostomic funnels opening into a lymph cavity, as we find in the mesonephros of *Rana ;* and, lastly, the ureter is also a separate structure, not related in any way to the old segmental duct.

The essential male reproductive organs are the testes. In the embryo these are situated on the latero-dorsal abdominal wall just behind the kidneys, and like them are asymmetrical, the right lying in front of the left. As the animal reaches maturity, however, they migrate backwards and finally lie in extensions of the body cavity, the **scrotal sacs,** which appear externally as small pouch-like projections of the body wall in the perineal region. The aperture joining the cavity of the sac to the abdomen is termed the **inguinal canal,** and the two cavities are always in open communication through it. Of course the testis was attached to the body wall in its original position by a fold of peritoneum, and there, too, it received its vascular and nervous connections. These obviously could not be broken, and so we find a strand of connective tissue with a nerve, an artery and a vein, attached to each testis and passing up through the inguinal canal to the primitive position of that body. The strand so formed is termed the **spermatic cord.**

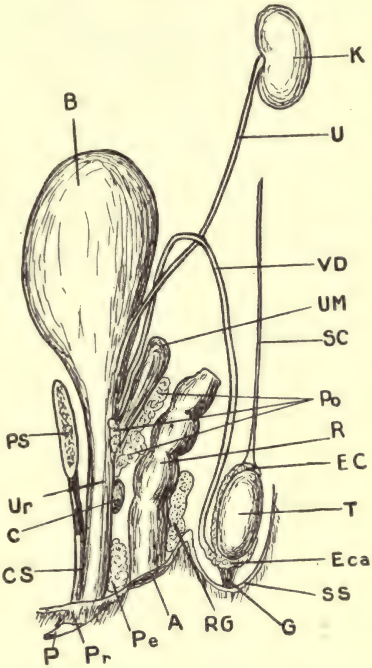


FIG. 110.—Diagram of male urogenital system of *Lepus*.

A., anus ; B., urinary bladder ; C., Cowper's gland ; C.S., corpus spongiosum ; E.C., caput epididymis ; E.Ca., cauda epididymis ; G., gubernaculum ; K., kidney ; P., penis ; Pe., perineal gland ; Po., prostate gland ; Pr., prepuce ; P.S., pelvic symphysis ; R., rectum ; R.G., rectal gland ; S.C., spermatic cord ; S.S., scrotal sac ; T., testis ; U., ureter ; U.M., uterus masculinus ; Ur., urethra ; V.D., vas deferens.

The testes themselves are oval pinkish-white bodies lying wholly within the scrotal sacs ; it is possible, however, to pull them through the inguinal canal into the abdominal cavity by means of the spermatic cord, but in so doing the scrotal sac will also be inverted, since they are attached to its posterior wall. Attached along the inner side of each testis is an irregular convoluted tubular mass,

the **epididymis,** in which three regions may be distinguished. The first is a rounded mass of this tissue, the **caput epididymis,** closely adherent to the anterior end of the testes near the attachment of the spermatic cord. The second is a narrow band passing along the medial side of the testis, and the third is a larger, somewhat conical mass, the **cauda epididymis,** attached to the posterior end of the testis. It is the cauda that is attached to the wall of the scrotal sac by means of a short strand of connective tissue, the **gubernaculum.**

Developmentally we find that the epididymis is the persistent highly modified remains of the mesonephros of the embryo, and its tubules grow into the testis constituting the vasa efferentia. The vas deferens is then the old mesonephric duct. The **vasa deferentia** arise from the cauda epididymis, pass through the inguinal canal into the abdominal cavity to a position on the outside of the ureters. They loop over the ureters ventrally and then run back on the dorsal side of the bladder to open into its neck below the ureters. From this point on there is one common duct for both the urinary and genital products, and it is termed the **urethra.** A median, short thick-walled sac, the **uterus masculinus,** opens into the urogenital canal, as the urethra may be called, a little lower down, and the canal then passes on ventral to the end of the rectum, and immediately dorsal of the pelvic symphysis to be continued outside the body in the penis. The **penis** or male copulatory organ is a short rod of tissue projecting from the ventral end of the perineum, but it is not conspicuous, since its free end is enclosed in a fold of skin, termed the **prepuce.** The posterior wall of the penis is formed of a very characteristic vascular tissue, the **corpus cavernosum,** while its ventral wall contains two closely apposed rods of firmer tissue, the **corpora spongiosa,** which diverge in the substance of the abdominal wall and are attached one to each ischium. The dorsal wall of the urethra just below the uterus masculinus bears a gland, the **prostate,** composed of four or five lobes which open into the urogenital canal on each side of a median papilla, the **verumontanum,** lying just below the aperture of the uterus. Still lower down are a pair of small ovoid bodies, **Cowper's glands,** one on each side of the dorsal surface of the urethra.

The rectum is a muscular thin-walled tube lying close to the urethra, but opening to the exterior by an entirely separate aperture, the anus. On its dorso-lateral walls it bears a pair of long, pale yellow bands of tissue, the **rectal glands.** On each side between rectum and urethra is a small **perineal gland** of a dark colour which opens on to a shallow depression, the perineal sac on the perineal area. It produces a secretion which is responsible for the characteristic smell of the rabbit.

The urinary organs of the female are practically the same as in the male save for a slight difference in the position of the openings of the ureters into the bladder, but the reproductive organs are naturally entirely different. The essential female organs are the **ovaries,** small oval bodies about three-quarters of an inch long, attached to the dorsal body wall by folds of the peritoneum, the **mesometria,** just behind the kidneys. On their surface can be seen semi-transparent rounded projections, the **Graffian follicles,** which are vesicular structures containing the ova, and they vary in size in accordance with the state of their development.

The **oviducts,** which are the much developed and modified pronephric ducts, have three distinct portions. The anterior end takes the form of a narrow, somewhat convoluted tube, the **Fallopian tube,** that opens into the cœlom quite close to the ovary, and has its opening furnished with a membranous funnel whose walls are much folded. The succeeding portion is greatly enlarged, and has thick muscular walls. This is the **uterus,** wherein the eggs undergo their development and the embryos are retained until they are born, so that the size of the two uteri depends upon whether they contain embryos or not. Each **embryo** or **fœtus** is actually attached to the uterus by the intimate union of an outgrowth from itself and a special receptive thickening of the uterine wall. The highly vascular mass of the tissue formed in this way partly from the fœtus and partly from the parent is termed the **placenta,** and it is the organ by means of which nutriment and oxygen are conveyed to the fœtus and carbon dioxide and nitrogenous waste matters removed. The

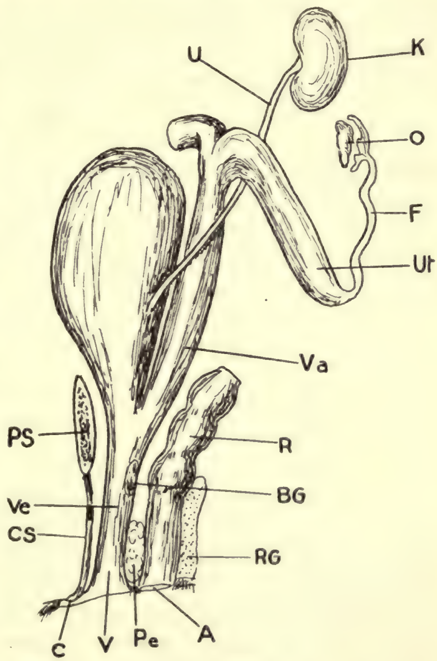


FIG. 111.—Diagram of female urogenital system of *Lepus*.

A., anus ; B., urinary bladder ; B.G., glands of Bartholini ; C., clitoris ; C.S., corpus spongiosum , F., Fallopian tube ; K., kidney ; O., ovary ; Pe., perineal gland ; P.S., pelvic symphysis ; R., rectum ; R.G., rectal gland ; U., ureter ; Ut., uterus ; V., vulva. Va., vagina ; Ve., vestibule.

uteri open by separate projecting apertures, the **ossa uteri,** into the succeeding portion of the genital tract, the **vagina**, which is a median unpaired structure representing the fused distal ends of the old pronephric ducts. Uteri and Fallopian tubes are attached to the dorsal wall of the abdominal cavity and held in place by a stout fold of peritoneum, termed the **broad ligament.** The vagina passes backwards to open into the neck of the bladder, so that from this point on, as in the male, we have a common urogenital duct here termed the **vestibule.** Its walls are very vascular, corresponding to the corpus spongiosum of the male. In the anterior median wall is a small rod-like body, the **clitoris,** corresponding with the penis in the male, and terminating externally in a soft sensitive spot, the **glans clitoridis.** Internally two small corpora spongiosa pass back from it to bifurcate in the abdominal wall and become attached to the ischia. The actual external opening is termed the **vulva,** and it is guarded by two lips. No glands corresponding to the prostate of the male are present, but Cowper's glands are represented by two areas containing the small glands of **Bartholini.** Perineal and rectal glands are present as in the male. and the urogenital tract is similarly related to the rectum.

Ductless Glands.

Before passing on to consider the nervous system it will be as well to glance quite briefly at the ductless glands. As in the frog, we shall include under this heading not only the glands in the strict sense of the term, but also the lymphoid organs.

The Spleen.—This is a dark red elongated body attached to the dorsal side of the cardiac end of the stomach by a side fold of the mesentery, the **gastro-splenic omentum.** It is the largest of the hæmolymph organs, and is enclosed in a quite distinct capsule composed of a mixture of fibrous and non-striate muscular tissue. From this capsule strands of tissue, the **trabeculæ,** pass inwards to ramify through the mass of the organ which is mainly composed of a soft tissue termed the **splenic pulp,** which contains several varieties of characteristically shaped cells. It is plentifully supplied with blood-vessels, whose arterioles are surrounded by denser lymphoid tissue that here and there swells out to form nodules often spoken of as Malpighian corpuscles.

The Tonsils.—These are also composed of masses of lymphoid tissue covered over by a stratified mucous membrane, the surface of which is pitted with tiny pores leading into tube-like recesses known as the crypts of the tonsil.

The Thymus.—This organ is a fairly large, soft pinkish mass lying in the anterior end of the thoracic cavity around the bases of

the main blood-vessels. It is relatively much larger in a young animal and may then even partly cover the heart. When examined in microscopic sections it is seen to be composed mainly of a lymphoid tissue. It appears to be concerned with nutrition and metabolic activities.

The Thyroid Gland.—This, the first of the ductless glands, is a soft dark-coloured body situated at the anterior end of the trachea. It is composed of two fairly large flat lateral lobes connected across the mid-ventral line by a thin strand of its own tissue closely attached to the trachea just below the thyroid cartilage. It is also subject to considerable variation in size. It is found to consist of an interlacing framework of connective tissue, which also forms a capsule and binds together a number of spherical vesicles. The walls of these vesicles are composed of a characteristic cubical glandular epithelium, and the secretion of their cells is found to fill the vesicular cavities with a readily coagulable fluid, which with its surrounding cells gives to the section of this body a striking appearance. It has already been noted that this secretion contains a protein rich in iodine and apparently plays an important rôle in katabolic activities.

Near each thyroid is a pair of small bodies termed the parathyroids, which are not composed of such typical glandular tissue. In addition to these there are certain other small accessory parathyroids in different places, sometimes included in another body. Their function is but little understood.

The Supra-renal Bodies.—In the rabbit these bodies are not directly connected with the kidney as in man, but lie a short distance away at the point where the renal vein of the same side flows into the post-caval. They are conspicuous light yellow-coloured bodies composed of two distinct varieties of tissue, termed the cortex on the outside and the medulla within.

The Pituitary Body.—This body is lodged within the sella turcica in the floor of the cranium, and is separated from the brain itself by the interposition of a tough double fold of the dura mater save at one point where it joins on to the infundibulum coming from the floor of the third ventricle. When examined microscopically three distinct regions can be distinguished. They are termed the **pars nervalis,** the **pars intermedium** and the **pars glandularis.** The latter is composed of typical glandular cells, and it arises in the embryo from an outgrowth of the dorsal wall of the stomodœum or mouth cavity which becomes completely cut off from the cavity in the course of development. It produces an important internal secretion whose function has been discussed briefly when considering this body in the frog.

The ovaries and testes also must be regarded as ductless glands,

for in addition to their primary function, that of producing the germ cells, they also secrete substances which play important parts in the development and activity of other parts of the body. Among other things they affect the development of what are termed the secondary sexual characters, that is to say, structures which, while not actually of value in reproduction, serve as distinguishing marks of the two sexes. These are very common in birds where the male is often of quite a different plumage from the female. As an example of the action of the gonads we may consider the case of horns in certain mammals. If the testes be removed from the young animal it does not grow horns even when of full size. Similar instances of other structures behaving in this way could be cited, but this one is sufficient to indicate the mode of action of the gonads as ductless glands.

CHAPTER XIII

LEPUS CUNICULUS—(*continued*)

The Nervous System and Sense Organs—The Mammalian Brain.

As in the lower forms, we find the whole of the central nervous system provided with a series of protective coverings, the **meninges.** The outermost of these is the **dura mater,** a tough fibrous membrane which lines the cavity of the cranium and neural canal. This dips down into the fissure between the cerebral hemispheres forming a sort of median membranous partition, the **falx cerebri ;** it also dips down in a similar way between the hinder end of the hemispheres and the cerebellum, thus giving rise to a transverse partition, the **tentorium.** In some mammals one or both of these folds may become ossified, and so give rise to thin bony plates attached to the inside of the cranium and dipping down into the fissures of the brain. Underlying the dura mater is a small **sub-dural lymph space,** and then a delicate **arachnoid membrane,** which is composed of a close felting of connective tissue. Finally, we have the innermost membrane, the **pia mater,** also delicate and extremely vascular. This invests closely the whole of the nervous matter dipping down into all the grooves of the brain and spinal cord.

The central nervous system is divisible into the brain and spinal cord, and the nervous tissue of which it is composed is divisible into grey matter and white matter as in all vertebrates. In the brain the former is on the outside, constituting the cortex, and the latter is inside, while in the spinal cord their positions are reversed. The grey matter is mainly composed of nerve cells with non-medullated fibres, and the white is formed entirely of fibres most of which are medullated.

Brain.

The brain of the rabbit is small and somewhat highly specialised, so that for more detailed investigation it is better to take the brain of a larger animal such as the sheep, and only consider the main outlines of its structure in the rabbit. The same main divisions of the brain that we have already seen in *Scyllium*

and *Rana* are also to be found in *Lepus*, but the relative size of the parts is very different, so that the brains as a whole are very dissimilar in external appearance. Perhaps the most striking difference is the enormous development of the cerebral hemispheres in *Lepus*, where they form a large part of the total mass of the whole brain. There is no doubt that mammals owe their dominant position in

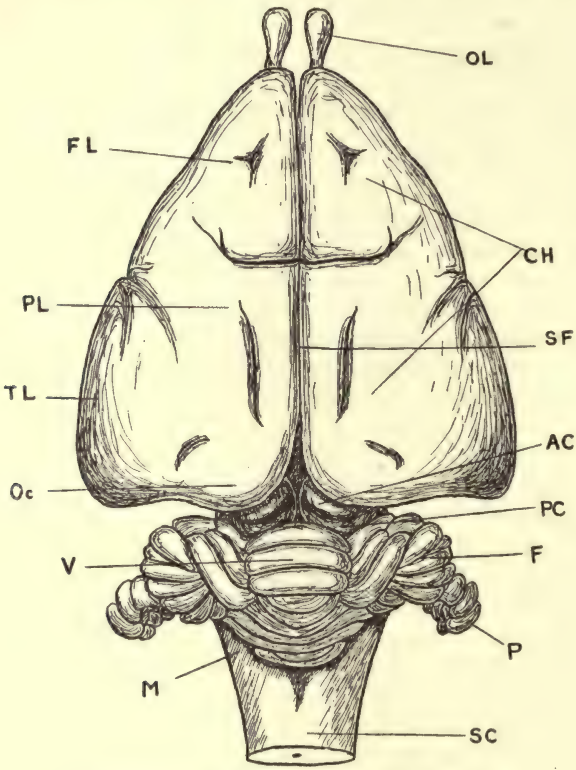


FIG. 112.—Brain of *Lepus*. Dorsal view.

A.C., anterior quadrigeminal body ; C.H., cerebral hemisphere ; F., flocculus ; F.L., frontal lobe ; M., medulla ; Oc., occipital lobe ; O.L., olfactory lobe ; P., paraflocculus ; P.C., posterior quadrigeminal body ; P.L., parietal lobe ; S.C., spinal cord ; S.F., sagittal fissure ; T.L., temporal lobe ; V., vermis.

the animal kingdom to-day to the large development of this region of the brain and the increase in intelligence that accompanies it.

The front end of the brain, the **telencephalon,** is expanded into the large cerebral hemispheres which form the anterior two-thirds of the brain and may be spoken of together under the inclusive term **cerebrum.** Both from the dorsal and lateral aspects they

present the shape of rounded triangles with their blunt apices directed forward. Internally they are hollow, containing the lateral ventricles which communicate posteriorly through the foramina of Munro with the third ventricle. Externally their convexly rounded surfaces are markedly shallow grooves, the **sulci**, one of which, lying at the side, is rather more marked than the remainder and divides the hemisphere into an anterior **frontal lobe** and a posterior **parietal lobe**, from which a ventral descending area, the temporal lobe, is marked off by another distinct sulcus. The two hemispheres are separated in the mid dorsal line by the deep **sagittal fissure**, in which is the falx cerebri, and if they are pressed apart it will be seen that a little way down their posterior ends are held together by a broad transverse band of tissue, the **corpus callosum**, which joins the nervous centres of the two sides of this part of the brain. This band of fibres is peculiar to the higher mammals, not being found outside that class, and it is even absent in the two lowest orders of the Mammalia, viz. the Monoteremes and the Marsupials. On the anterior ventral surface of the telencephalon are two club-shaped bodies, the **olfactory lobes**, whose swollen extremities project beyond the front end of the cerebral hemispheres. The first pair of cranial nerves, the olfactory, leave their anterior surfaces as a series of fibres.

The next portion of the brain, the thalamencephalon, contains the third ventricle, and is roofed by the anterior choroid plexus, but it is not visible from the dorsal side, since it is entirely overlain by the posterior ends of the hemispheres. The **epiphysis cerebri** or **pineal body** coming from its postero-dorsal surface can sometimes be made out between the divergent posterior lobes of the cerebrum. On the ventral surface of this region of the brain we find the **optic chiasma**, the **infundibulum** and the **pituitary body** or **hypophysis cerebri**. In spite of its small size and inconspicuousness we shall find when we come to consider the details of its structure and relationship that it is a most important part of the brain.

The **mesencephalon** or mid brain is also largely hidden by the hemispheres, but can be seen easily if their hinder ends are pushed apart. On the dorsal side are two pairs of rounded bodies, the **corpora quadrigemina** or **optic lobes**, homologous with the corpora bigemina of the dogfish or frog, but subdivided. The ventro-lateral part of this region is constituted by the **crura cerebri**, two smooth bands of fibres passing, backwards and the hollow within it is the iter a tertio ad quartum ventriculum.

The **cerebellum** is the well-developed dorsal region of the **metencephalon**. It forms a transversely elongated mass consisting of a median lobe, the **vermis**, and two **lateral** or **floccular lobes**, which

bear at their postro-lateral corners two small, easily detached lobes, the **paraflocculi,** situated within the floccular fossæ of the cranium. The whole of the surface of the cerebellum is marked by close set, almost parallel, and for the most part transverse folds or sulci. The ventral portion of the metencephalon is composed of a trans-

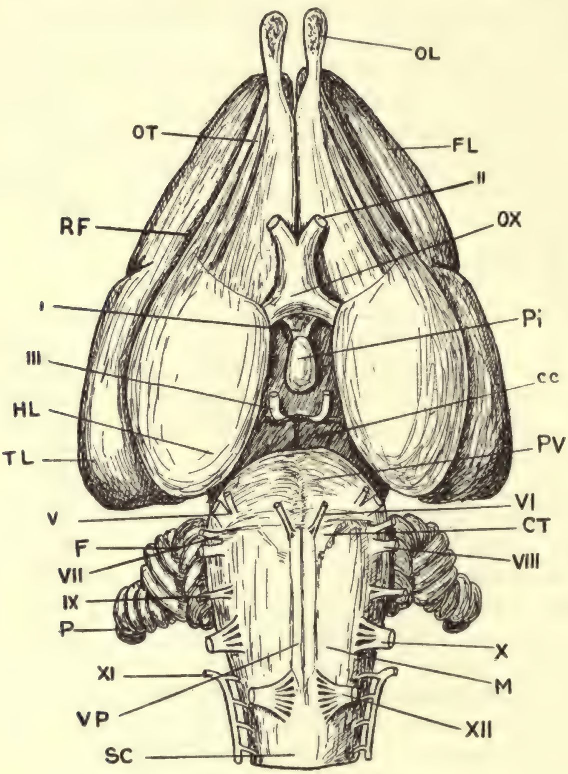


FIG. 113.—Brain of *Lepus*. Ventral view.

C.C., crus cerebri; C.T., corpus trapezoideum; F., flocculus; F.L., frontal lobe; H.L., hippocampal lobule; I., infundibulum; M., medulla; O.L., olfactory lobe; O.T., olfactory tract; O.X., optic chiasma; P., paraflocculus; Pi., pituitary body; P.V., pons Varolii; R.F., rhinal fissure; S.C., spinal cord; T.L., temporal lobe; V.P., ventral pyramids; II.-XII., roots of spinal nerves.

versely running broad band of fibres, the **pons Varolii,** which connects the two sides of the cerebellum across the mid ventral line.

The **myelencephalon** is composed of a somewhat flattened mass, the **medulla oblongata,** whose roof is formed by the posterior choroid plexus which, however, is hidden beneath the enlarged cerebellum. On its ventral surface we can recognise two narrow longitudinal

bands, the **ventral pyramids,** lying one on each side of the shallow median ventral fissure. Outside these at the front end, that is, immediately behind the pons, are to be distinguished a pair of areas termed the **corpora trapezoidea.** Posteriorly the medulla passes on into the spinal cord without any sharp line of demarcation.

There is but one cavity common to both the metencephalon and myelencephalon, and that is the fourth ventricle.

Cranial Nerves.

Twelve large pairs of nerves leave the cranium in the rabbit, and they are commonly termed the cranial nerves, but, strictly speaking, one of them, the eleventh or spinal accessory, is largely composed of fibres coming from the spinal cord. The points of origin of these nerves, while they can be made out in the rabbit, are much better studied in a larger brain, and they will, therefore, be considered later, although it should be borne in mind that they arise in the same relative position in both rabbit and sheep, and, indeed, the first ten are constant throughout the chordate series from dog-fish to man himself. It should be borne in mind that although we speak of ten cranial nerves in lower vertebrates and twelve in the higher forms, there is present in all of them from lowest to highest another nerve right at the anterior end. This is termed the **nervus terminalis,** and it arises from the front median portion of the telencephalon and passes forward in the neighbourhood of the olfactory lobe to be distributed in the region of the internasal septum. Its exact functional significance has not yet been ascertained, though it is present in all forms. Again, we find in all vertebrates a second small nerve, the **vomero-nasalis** or **septalis,** which arises not far from the other, but developmentally just behind the olfactory. This, too, is distributed in the neighbourhood of the nasal septum, and its function is not yet understood. So that to be strictly accurate we should say there are twelve cranial nerves in the lower Chordates such as *Rana* and *Scyllium*, and fourteen in the higher forms like *Lepus*.

We may now consider briefly the distribution of these nerves in the rabbit.

The **nervus terminalis** is a small nerve, comprising only a few fibres, passing out on the mesial wall of the cerebral hemisphere in the sagittal fissure. It runs through the cribriform plate with the fibres of the olfactory nerve, and spreads out to help to form a plexus, in company with the nervus septalis, in the neighbourhood of the nasal septum and Jacobson's organ.

The **olfactory nerve,** composed of numerous branches, ramifies all over the olfactory membrane in the nasal chamber and covering

the turbinal bones. It is purely sensory in function and subserves the sense of smell. Its fibres pass in numerous bundles through the cribriform plate to enter the olfactory bulb.

The **vomero-nasal** or **septal nerve** is a small nerve whose fibres also pass through the cribriform plate and, as just noted, form a plexus with those of the nervus terminalis.

The **optic nerve** enters the orbit and runs straight to the eye. It penetrates the sclerotic coat, the choroid coat and the retina, and at the blind spot spreads out radially to be distributed over the internal surface of the retina. It is a purely sensory nerve and subserves the function of sight.

The **oculomotor nerve** enters the orbit through the foramen lacerum anterius. It is a motor nerve, and breaks up to be distributed to the internal, superior and inferior recti and the inferior oblique muscles of the eye-ball.

The **pathetic** or **trochlear nerve** is also a motor nerve accompanying the third into the orbit, but passing across its inner wall to the superior oblique muscle.

The **trigeminal nerve** is a very large mixed nerve containing both sensory and motor fibres. A short distance from its origin it swells out to form the large **Gasserian ganglion,** from which its three main trunks are given off, viz.: the ophthalmic, the maxillary and the mandibular. The first two of these leave the skull by the foramen lacerum anterius, while the last leaves through the anterior portion of the foramen lacerium medium, that is, the portion that in many mammals is a separate aperture, the foramen ovale.

The **ophthalmic trunk** is a large nerve which crosses the mesial border of the orbit and, after giving off twigs to the tissues in the region of the eyelid and lachrymal region, reaches the front end of the dorso-mesial wall of the orbit. Here it splits into two branches, the nervus frontalis and the nervus naso-ciliaris. The **frontalis** goes through the notch at the front end of the supra-orbital process of the frontal bone to the skin and subcutaneous region of the upper eyelid. The **naso-ciliaris** passes through the internal orbital foramen to the nasal region.

The second trunk, the **maxillary,** passes along the inner border of the orbit and the main part of it goes through the infra-orbital canal as the **infra-orbital nerve,** passing to the front end of the upper lip and the snout, and also giving branches to the anterior teeth. Within the orbit it gives off at the hinder end a subcutaneous branch going outwards to the skin; a **sphenopalatine branch,** which after a short distance enlarges to form the **sphenopalatine ganglion** and the **posterior dental nerve** going to the hindermost teeth. From the sphenopalatine ganglion are given off several naso-sphenopalatine

nerves which pass through the anterior palatine foramen and so reach the nasal region. The ganglion also gives off palatine nerves, of which the **anterior palatine** goes through the posterior palatine foramen to supply the mucous membrane of the hard palate, while the **posterior palatine** branches supply the soft palate.

The **mandibular** or **inferior maxillary** nerve leaves the cranium, as noted, through the foramen lacerum medium, and almost at once gives off twigs supplying the pterygoid, masseter and temporal muscles of the head and the adjacent tissues. After a short course it divides into two branches, the lingual and the mandibular. The lingual nerve passes downwards, and below the level of the tympanic cavity receives an anastomosing branch from the seventh nerve. It then passes forwards and inwards to supply the tissues of the tongue. The mandibular nerve passes a little more posteriorly and, further, ventrally to the inner surface of the ramus of the mandible into the substance of which it penetrates through the inferior dental foramen, thus reaching the teeth. Its terminal branches issue on the outside of the anterior end of the ramus through the mental foramen as the **nervus mentalis** to supply the tissue of this region.

The **abducens** is quite small, and leaves the cranium through the foramen lacerum anterius in company with the first two branches of the trigeminal, and passes postero-laterally a short distance across the orbit to supply the external rectus muscle.

The **facialis** is another large mixed nerve whose roots unite to form the **geniculate ganglion,** and the greater portion of it leaves the cranial cavity by the internal auditory meatus, and the skull by the stylo-mastoid foramen. From the ganglion three main branches come off. The first is the **chorda tympani,** the branch which, as we have seen, anastomoses with the lingual branch of the trigeminal. It passes posteriorly to the tympanic cavity. The second is the **ramus palatinus,** termed also in mammals the **nervus petrosus superficialis major,** which passes forwards above the tympanic cavity to the palatine region and sends a branch to anastomose with the maxillary branch of the trigeminal at the sphenopalatine ganglion. The main **hyomandibular branch** of the nerve passes behind the tympanic cavity and is distributed generally to the tissues of the dorsal and ventral sides of the hinder end of the head, the external mandibular region and to the hyoid region.

The **auditory nerve** also leaves the cranial cavity by the meatus auditorius internus, and at the end of this canal divides into a **cochlear branch** distributed mainly to the cochlea, and a **vestibular branch** serving the majority of the remaining part of the membranous labyrinth.

The **glosso-pharyngeal nerve** leaves the skull through the foramen

lacerum posterius in company with the tenth and eleventh nerves and the internal jugular vein. It passes downwards between the jugular vein and the internal carotid artery and then turns forward to spread out in the tongue, tonsils and pharyngeal region.

As we have seen, the **vagus nerve** leaves the skull through the foramen lacerum posterius, and it swells out shortly after to form a distinct **vagus ganglion.** It descends the neck external to the common carotid artery into the thoracic cavity, and then through this alongside the œsophagus into the abdomen, where in proximity to the stomach it breaks up. Just beyond the ganglion at the anterior end of the neck it gives off the **anterior laryngeal nerve,** a small trunk running inwards and forwards dorsal to the carotid artery, to be distributed to the larynx and the crico-thyroid muscle. A second branch, the **depressor nerve,** arises generally from the preceding, but it may come directly from the main trunk at or near the same point. This passes back along the neck mesial to the main vagus trunk and dorsal to the common carotid artery to go to the heart. It receives its name from the fact that stimulating it produces a depression of the beating of the heart. The last noticeable branch from the vagus is the **posterior** or **recurrent laryngeal nerve,** which is differently disposed on the two sides. On the right it leaves the vagus just in front of the sub-clavian artery, then loops around this vessel and finally takes up a position at the side of the trachea and passes forward along it to supply most of the laryngeal muscles. On the left side it comes off further down, behind the sub-clavian artery and actually in the thoracic cavity. It loops around the arch of the aorta and so reaches its position by the side of the trachea. This curious looping of the nerves is comprehensible when we consider the development of this region. Originally the heart is situated much more anteriorly, and its carotid and systemic trunks, representing the third and fourth of the afferent branches of a fish, *e.g. Scyllium,* are morphologically in front of the point of origin of the larynx. The nerves then run behind these arteries. In the course of development the heart, and with it the arteries, shifts backwards and consequently the nerve becomes pulled out into a loop.

While traversing the thorax the main trunk of the vagus gives off branches to the lungs, œsophagus and heart, the last named forming a plexus around the roots of the aorta and pulmonary artery.

The **spinal accessory nerve** is a short nerve also leaving the cranium by the foramen lacerum posterius. It passes almost vertically downwards lateral to the vagus, and is distributed to the sterno-mastoid and other adjacent muscles. A short distance along it gives off a ramus internus which joins the vagus.

The **hypoglossal nerve** is a stout trunk that comes out of the skull by the condylar foramen and runs backwards lateral to the preceding nerves and slightly inwards. When it reaches a point near the place where the common carotid artery splits into its internal and external branches it divides into two. The anterior nerve crosses the internal carotid artery ventrally and runs forward parallel to and outside the external carotid, and also to the posterior cornu of the hyoid bone to the base of the tongue, which it serves together with the muscles of that region. The posterior branch passes backwards, and after a short distance crosses the common carotid ventrally and breaks up into branches supplying the muscles of the hyoid and thyroid region. Some of these nerves receive fibres also from the first and second spinal nerves.

Spinal Cord.

The spinal cord passes back without visible line of demarcation from the hinder end of the medulla oblongata as a

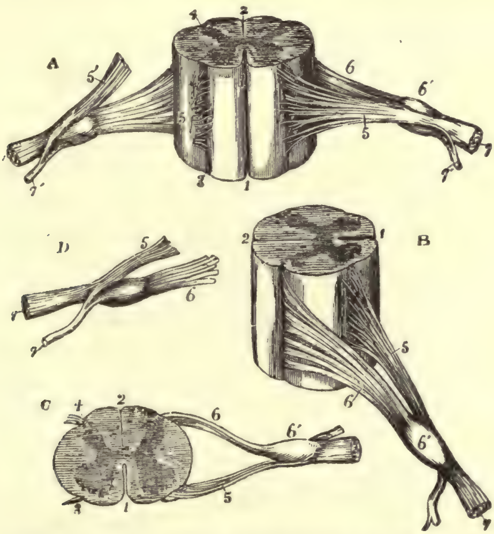


FIG. 114.—Roots of a spinal nerve issuing from the cord.—From Quain. A, from before ; B, from the side ; C, from above ; D, the roots separated.

1, ventral fissure ; 2, dorsal fissure ; 3 and 4, lateral grooves of the cord ; 5, ventral root 6, posterior root ; 6′, dorsal ganglion ; 7, the united or compound nerve ; 7′, the dorsal branch. In A one ventral root is divided and turned upwards.

long rod, at first somewhat oval, but soon nearly round, the whole length of the neural canal. The side walls of the posterior end of the roof of the fourth ventricle meet together in the mid-dorsal line,

and their junction is marked by the formation of a groove. This continues on down the cord as a narrow but quite deep cleft, the **dorsal fissure.** On the ventral side is another groove, the **ventral fissure,** not quite so deep and somewhat wider than the dorsal one. As previously noted, the same meninges that we find in the brain surround the spinal cord, but the arachnoid is divided into two layers, separated by quite a large **sub-arachnoid space,** which communicate on the dorsal side by a septum.

The **canalis centralis** is very much reduced, and its lumen appears as a tiny space situated nearer the end of the dorsal fissure than the ventral. It is lined by **ependymal epithelium** continuous with that of the brain cavities. In transverse section the cord is seen to be composed of a characteristic H-shaped arrangement of grey matter surrounded by white matter. The canalis centralis lies in the middle of the transverse bar of the H, and has above it a band of transverse fibres, the **dorsal commissure,** and below it a wider but similar band, the **ventral commissure.**

Spinal Nerves.

Throughout the whole of its length the spinal cord gives off the paired segmental **spinal nerves,** leaving the vertebral column by the intervertebral foramina. Each arises as in all vertebrates by two roots, a **dorsal root** related to the **dorsal horn** of the grey matter, and a **ventral root** issuing from the **ventral horn.** The dorsal root bears, a short distance from its origin, the **dorsal root ganglion,** almost immediately beyond which the two roots unite to form a common trunk. The common nerve so constituted leaves the vertebral column and gives off a small **ramus dorsalis** passing to the muscles and skin of the dorsal body region and tiny strands to the sympathetic chain. The main part goes on as the **ramus ventralis** to be distributed to the more ventrally situated portions of the body.

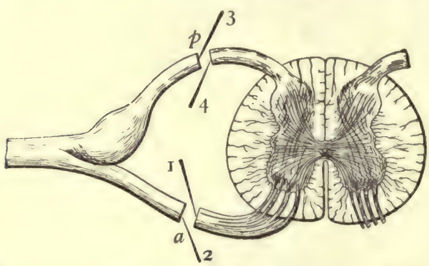


FIG. 115.—Illustrating the functions of the roots of the spinal nerves.—From Furneaux

a., ventral root; *p.*, dorsal root.
Divided at a.—Irritated at 1: no result. Irritated at 2: contraction of muscles supplied with fibres from the root.
Divided at p.—Irritated at 3: no result. Irritated at 4: pain produced.

The nature of the two roots of the spinal nerves is a matter of some interest. If the common trunk after the point of fusion be

cut and the ends stimulated, it will be found: (1) that from the distal end a message is conveyed to the muscles showing that it contains motor or efferent fibres conducting impulses away from the central nervous system, and (2) that from the proximal end a message or sensation is carried to the brain, indicating that some of its fibres are afferent or sensory. The whole nerve is therefore mixed, containing both motor and sensory fibres.

If the dorsal root be cut between the ganglion and the cord, and stimulated, it will be found: (1) that from the proximal end a sensory message is conveyed to the brain, and (2) that from the distal end no results can be obtained. The dorsal root, therefore, is entirely a sensory root and, like all nerve fibres, its constituents can convey a message in one direction only.

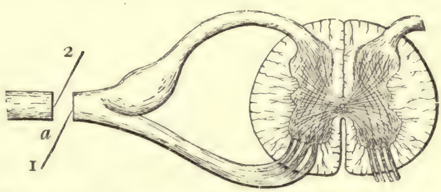


FIG. 116.—Illustrating the functions of the spinal nerves.—From Furneaux.

Divided at a.—Irritated at 1: pain. Irritated at 2: muscular contraction.

If the ventral root be severed before its point of union we shall see: (1) that stimulation of the proximal end produces no response, so that it contains no sensory or afferent fibres, but (2) that stimulation of the distal end results in movement. The ventral root is, therefore, a purely motor nerve.

The distribution of the spinal nerves calls for little notice, and we need only deal with certain small points. The third spinal nerve gives off a large branch termed the **great auricular nerve,** that runs up the postero-lateral border of the pinna supplying the neighbouring tissues. The fourth spinal nerve gives off a fairly large branch that runs backwards below the roots of the others receiving a tributary from the fifth nerve, and sometimes from the sixth also. The combined trunk passes into the thorax as the **phrenic nerve** to be distributed over the diaphragm. In certain regions, noticeably the axillary and lumbar, there is a certain amount of intercrossing of fibres from adjacent nerves constituting the brachial and lumbar plexuses respectively.

Sympathetic Nervous System.

The sympathetic nervous system is constituted in fundamentally the same way as in the frog, but it is somewhat more specialised, and the ganglionation of the two lateral trunks lying beneath the vertebral column is not quite so regular. As we have seen, each spinal nerve on emerging from the vertebral column

sends off a small twig to join the common trunk. The main trunk on each side is connected anteriorly with the sphenopalatine ganglion and communicates with the intra-cranial portions of the trigeminal, glosso-pharyngeal and vagus. Extra-cranially it is connected also with the hypoglossal. At the anterior end of the neck it lies close to the trachea, slightly dorsal and mesial to the carotid artery, and there enlarges to form an **anterior cervical ganglion,** partly in front of the vagus ganglion. It passes backwards, and at the hinder end of the neck just in front of the sub-clavian artery it enlarges to form a **median cervical ganglion.** The chain is connected with a plexus of sympathetic fibres in the heart, and then passes back into the abdominal cavity, where it is related to three median ganglionic enlargements. The first of these is the **cœliac ganglion,** lying between the cœliac and anterior mesenteric arteries. The second is the **anterior mesenteric ganglion,** situated just behind the similarly named artery. Fibres run back from this to a much smaller **posterior mesentric ganglion** lying in the mesentery just in front of the artery of the same name. These three ganglions, particularly the front two, are sometimes referred to as the solar plexus.

The fibres from the sympathetic chain are distributed to all the viscera and regulate the activity of the non-striate muscles so that the system is sometimes spoken of as the involuntary nervous system.

Sense Organs.

Little remains to be noted in regard to the sense organs, since they have already been dealt with sufficiently in other forms, and, indeed, the description of the eye given was based mainly upon that of a mammal.

The **olfactory organ** is very well developed and occupies the large anterior nasal chamber. Although a large space it is almost completely filled with the complicated turbinal bones, over all of which spreads the typical olfactory neuro-epithelium.

The details of the structure of the eye call for no further expansion, but it will be seen from the position that it occupies, well sunk in the deep orbit at the side of the skull, that each eye looks out to its own side, and that there is practically no overlapping of the two fields of vision as in our own case.

It is in the ear that we meet with the greatest advance over the conditions in *Rana*. In the first place the tympanic membrane is no longer upon the external surface of the skull, but has sunk down a considerable way, and the wide canal leading from it to the outside, *i.e.* the external auditory meatus, is enclosed in the tympanic bone. On the outside of the skull, in order to compensate for the loss

of accessibility, a trumpet-shaped structure, the external ear or pinna, is developed. This collects the sound waves and conducts them through the meatus to the tympanic membrane. A columella auris is not present, but its place is taken functionally by a chain of auditory ossicles, the malleus, the incus, the os orbiculare and the stapes, by whose agency the vibrations of the tympanum are transferred to the fenestra ovalis and so to the perilymph surrounding the membranous labyrinth.

The internal ear itself is also much modified. We find, as before, a vestibule relatively small and divided into a sacculus and utriculus. From it come off the three semicircular canals which, while differing somewhat from those in the lower forms, are essentially the same in structure and function. A small ductus endolymphaticus is also present, but it only runs a short distance and then swells out into a small blind enlargement, the **saccus endolymphaticus.** The most noticeable alteration is in the cochlea. In the frog this is a comparatively small projection from the wall of the sacculus, while in the rabbit it has developed into a very complicated structure much larger than the vestibule itself. The cochlea is coiled upon itself so as to resemble somewhat a snail shell, and its internal cavity is divided up into three separate compartments by longitudinally running partitions. It is not proposed to enter into a detailed discussion of the histology or anatomy of this structure, but it should be noted that it is probably to be regarded as a highly specialised organ for the appreciation of musical sounds.

The organs of touch and taste are very similar to those described previously, save that they, too, appear to reach a higher degree of development, and have a characteristic distribution, as we have seen in the case of the latter on the tongue.

This then concludes the account of the rabbit, which has been taken as a type of the class Mammalia, which is the highest class of animals now living or, so far as we know, has ever lived, and culminates in man himself. They are characterised above all by the great development of their brain, and in this, too, man outstrips all other forms. So that before leaving them it will be as well to consider this organ in slightly more detail in a larger form than *Lepus*.

The Brain of a Mammal—the Sheep.

For the more detailed study of the mammalian brain we may take that of the sheep. It has the advantage of being of a suitable size and readily procurable, also, in so far as we shall treat of it, the structures are fairly typically arranged. For the purposes of dissection it is best to use a brain that has been hardened for some time previously.

The meninges are readily studied in the sheep's brain, and with a little care they may be removed from the cranium intact with the brain. The falx cerebri is easily recognisable, although it only penetrates the sagittal fissure a very short distance save at its posterior end, where it joins the tentorium, which is well developed. In the thickness of these two folds lie venous sinuses which convey the blood away from the brain. They are termed the **sinus sagittalis** and the **sinus transversus** respectively. Turning now to the brain itself we find it to be a large ovoid structure of which the anterior three-quarters of the dorsal portion is constituted by the cerebrum.

Fore-Brain.

The large hemispheres are highly specialised outgrowths from the dorsal region of the telencephalon, and they extend so far back that they completely hide the thalamencephalon and mesencephalon. They are separated in the middle line by a well-marked sagittal fissure, and their well-rounded surfaces are covered with very distinct grooves or **sulci** dividing them off into a series of well-marked broad ridges, the convolutions or **gyri.** Certain of these sulci are of importance, since they serve to mark off the surface of the brain into more or less well-defined areas. The first of these is the **fissura cruciata,** which starts as a deep groove in the mid-dorsal line and passes transversely, following a slightly curved course and separates an anterior **frontal lobe** from a larger posterior **parietal lobe.** The second is the **fissura suprasylvia,** which arises in a Y-shaped union of two sulci just behind the fissura cruciata about half-way out, and runs at first backwards and then outwards and downwards over the side of the hemisphere ; in its posterior two-thirds it marks the boundary between the parietal and the descending **temporal lobe.** The third of them is the **fissura rhinalis,** which, although visible from the side, is best seen from the ventral aspect, as it starts just lateral to the olfactory lobe and passes backwards with a slightly bowed course to the hinder end of the hemisphere. The area on the inside of this is sometimes termed the **pyriform lobe,** and its hinder end distinguished as the **hippocampal lobule.** All the various grooves and ridges are formed by the folding of the wall of the cerebellum, and they have the result of giving a greatly increased surface. As has been noted before, the grey matter constituting the cortex is the seat of the actual nerve cells, and so by this means a much larger area is provided and so many more cells can be accommodated.

If the sagittal fissure be opened on the dorsal side, or if the median edges of the hemispheres be sliced off, the **corpus callosum** will be revealed. It is a transverse band of fibres occupying about two-

thirds of the total length of the cerebrum whose hemispheres project both in front and behind it. At the hinder end of the corpus will be seen the small **pineal body,** arising from the posterior dorsal end of

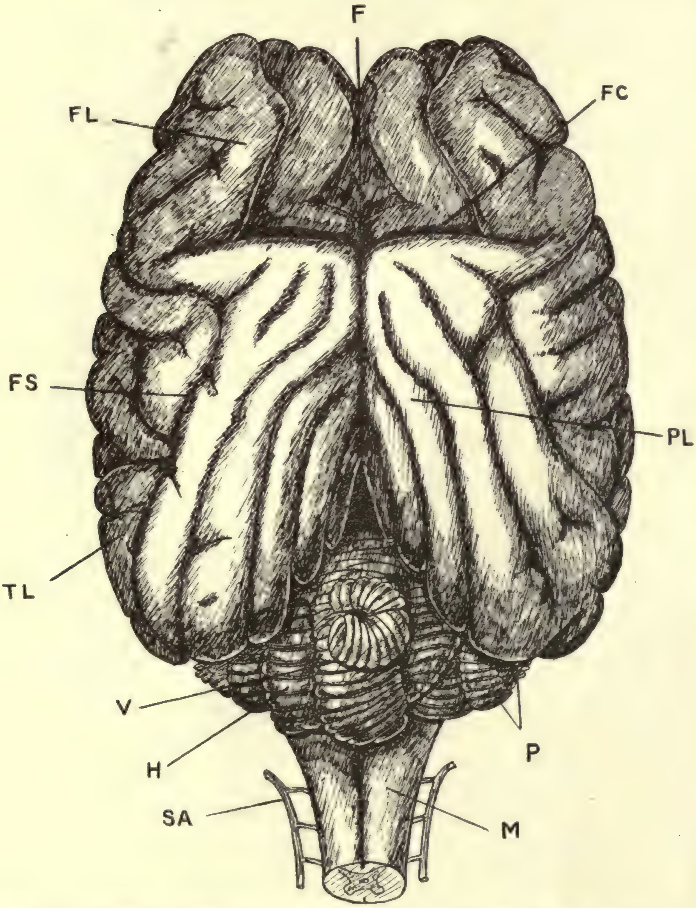


FIG. 117.—Brain of sheep, dorsal aspect, adapted from Burkholder.

F., fissure longitudinalis ; F.C., fissura cruciata : F.L., frontal lobe ; F.S., fissura suprasylvia ; H., hemisphærium cerebelli ; M., medulla ; P., paraflocculus ; P.L., parietal lobe ; S.A., spinal accessory nerve ; T.L., temporal lobe ; V., vermis.

the telencephalon and behind and lateral to it, the two anterior quadrigeminal bodies belonging to the mid-brain. The posterior quadrigeminal bodies lie just behind the anterior pair, but they are much smaller and hidden by the larger ones.

That portion of the cerebrum lying within the limits of the rhinal fissures may be regarded as the ventral surface of the telencephalon, and calls for notice owing to the presence thereon of

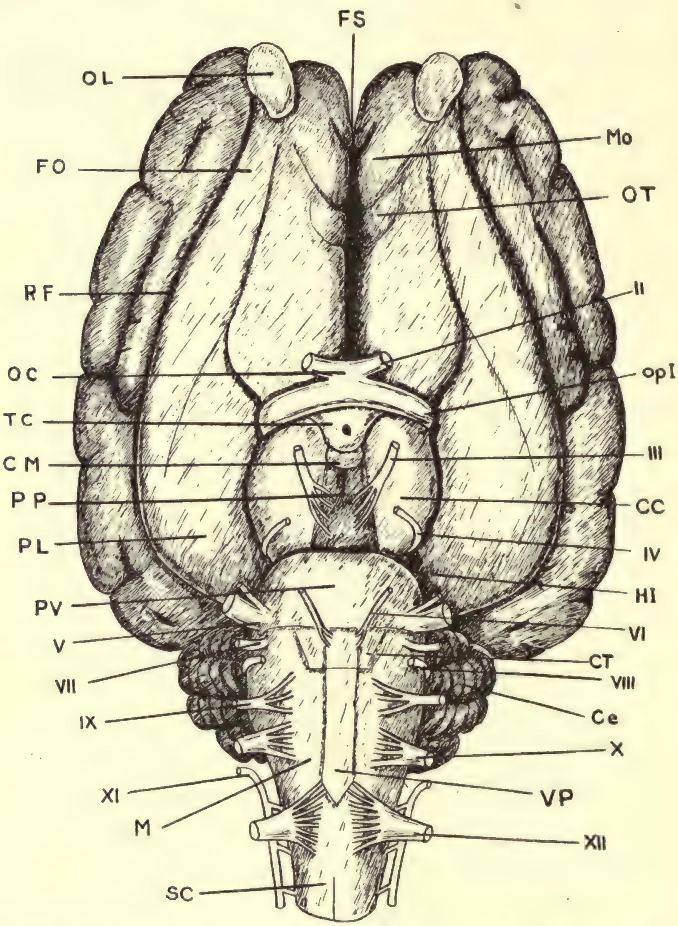


FIG. 118.—Brain of sheep, ventral aspect, adapted from Burkholder.

C.C., crus cerebri; Ce., cerebellum; C.M., corpus mammilare; C.T., corpus trapezoideum; E.O., external olfactory root; F.S., sagittal fissure; H.L., hippocampal lobe; M., medulla; M.O., median olfactory root; O.C., optic chiasma; O.L., olfactory lobe; Op.T., optic tract; O.T., olfactory tubercle; P.L., pyriform lobe; P.P., posterior perforated spot; P.V., pons Varolii; R.F., rhinal fissure; S.C., spinal cord; T.C., tuber cinereum; V.P., ventral pyramid; II.-XII., roots of cranial nerves.

certain important structures. Right at the front end, and projecting slightly beyond the hemispheres, are two obliquely directed **olfactory lobes,** completely separated by the sagittal fissure which

passes round the front end of the corpus callosum and back for some distance on the ventral surface. Each lobe sends back three roots to the front end of the pyriform lobe. Of these two, a distinct **lateral root** passing backwards and outwards, and a less distinct **median root** running backwards and inwards to disappear in the sagittal fissure, are discernible externally, while the third or **intermediate root** is internal. Just behind the limit of the median roots where they pass into the sagittal fissure is a small oval area, the **olfactory tubercle.** Behind this is an area limited externally by the inner margin of the lateral root, mesially by the sagittal fissure and anteriorly by the olfactory tubercle. This is known as the **anterior perforated spot,** because of the numerous branches arising from the anterior cerebral artery that here perforate the surface of the brain to supply its internal tissues. Posteriorly this area and the sagittal fissure are terminated by the prominent **optic chiasma,** from which arise the large optic nerves one on each side. The nerves are represented only by short stumps, as they have to be cut in removing the brain from the cranium. The chiasma is formed by two large curved bands of fibres, the **optic tracts,** which come from the base of the anterior quadrigeminal bodies and pass ventrally and slightly forwards to unite in the middle line.

Immediately behind the middle of the optic chiasma is a low median elevation, the **tuber cinereum,** lying on the floor of the third ventricle, the cavity of which is continued downwards as a short, somewhat conical canal, the **infundibulum,** into the tuber. When the brain is *in situ,* the fairly large oval **pituitary body** or **hypophysis cerebri,** which lies in the sella turcica, is almost completely separated from the brain by a double fold of the dura mater. It is attached to the tuber, and the infundibular cavity passes on into it. Generally in removing the brain from the cranium the pituitary body is left behind so that its position is marked by a perforation in the tuber. Behind the tuber is a second low eminence, the **corpus mammillare,** which marks the hinder end of the floor of the third ventricle and is divided into two corpora by a median groove in some animals. If the pituitary body remains attached to the brain it completely hides the corpus mammilare.

This, then, completes the structures visible on the outside of the fore-brain, and before passing on to the mid-brain it will be as well to study the internal anatomy of the prosencephalon. As it is a hollow structure we may start with the cavities. The lateral ventricles are a pair of symmetrically arranged hollows, one in each hemisphere, and as they arise as antero-lateral outgrowths of the fore-brain vesicle of the embryo they are lined by the ependyma, the characteristic epithelium that lines all the brain cavities and the

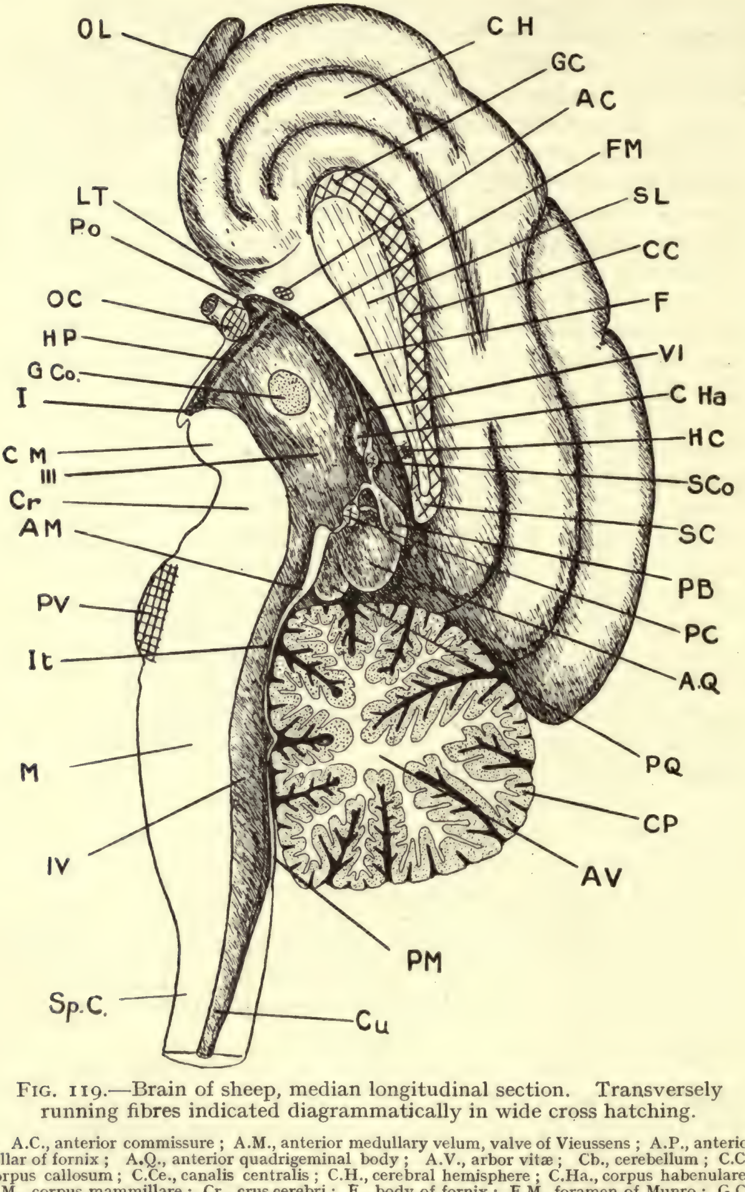


FIG. 119.—Brain of sheep, median longitudinal section. Transversely running fibres indicated diagrammatically in wide cross hatching.

A.C., anterior commissure ; A.M., anterior medullary velum, valve of Vieussens ; A.P., anterior pillar of fornix ; A.Q., anterior quadrigeminal body ; A.V., arbor vitæ ; Cb., cerebellum ; C.C., corpus callosum ; C.Ce., canalis centralis ; C.H., cerebral hemisphere ; C.Ha., corpus habenulare ; C.M., corpus mammillare ; Cr., crus cerebri ; F., body of fornix ; F.M., foramen of Munro ; G.C., genu of corpus callosum ; G.Co., grey commissure ; H.C., hippocampal commissure ; I., infundibulum ; It., iter ; L.T., lamina terminalis ; M., medulla ; O.C., optic chiasma ; O.L., olfactory lobe ; P.B., pineal body ; P.C., posterior commissure ; P.M., posterior medullary velum ; P.O., pre-optic recess ; P.Q., posterior quadrigeminal body ; P.V., pons Varolii ; S.C., splenium of corpus callosum ; S.Co., superior commissure ; S.L., septum lucidum ; Sp.C., spinal cord ; V.I., velum interpositum ; III. third and IV. fourth ventricles.

canalis centralis of the spinal cord, and which is derived from the inner cells of the original neural tube. Each lateral ventricle lies below the corpus callosum whose ventral fibres form its roof, and it is a fairly narrow irregularly shaped cleft with very well-marked anterior and descending horns. The **anterior horn** passes forwards and downwards, being somewhat ⌈-shaped in transverse section, gradually becoming reduced in size until finally as a small slit it passes up the olfactory stalk and enlarges slightly to form the ventricle of the olfactory bulb. The **descending** or **inferior lateral horn** of the ventricle runs backwards, outwards and downwards into the hinder region of the hemisphere, *i.e.* the temporal lobe. The region where the two horns join is sometimes termed the body of the lateral ventricle, and it opens into the third ventricle by a narrow vertical aperture, the **foramen interventriculare** or **foramen of Munro.**

The mesial wall of the anterior cornu below the corpus callosum is formed by a delicate semi-transparent membrane which comes to lie so close to its fellow in the middle line that the two join and form what is known as the **septum lucidum,** which is limited on the ventral side by a thickened mass of tissue, the fornix. In man there is a cleft-like cavity within the septum. The ventro-lateral wall of this cornu is composed of a thick important mass of nervous tissue known as the **corpus striatum,** from the striated appearance it presents in transverse section. The lateral and dorso-lateral walls of the anterior cornu is composed of the grey matter of the cerebral cortex and also of white matter arranged in a characteristic radiating manner to form the **corona radiata,** which is the lateral continuation of the corpus callosum.

The mesial, posterior and ventro-lateral walls of the descending cornu are formed by a large ganglionic mass, the **hippocampus,** and attached to this is the posterior pillar of the fornix. Its lateral and dorso-lateral walls are composed of the white matter underlying the cerebral cortex. In front of the pillar of the fornix a narrow strip of the wall of the ventricle becomes very thin, and it is continuous through the interventricular foramen with the epithelium of the roof of the third ventricle, immediately above which the highly vascular pia mater forms the anterior choroid plexus. This thin epithelium with its pia mater is deeply invaginated into the ventricle as a marked folded band of tissue, and so constitutes the **choroid plexus** of the **descending horn.** In removing the meninges this portion of the pia mater, together with the epithelium with which it is bound up, is usually torn away, so leaving what appears to be a curved slit-like opening, sometimes spoken of as the "choroidal fissure," leading from the ventricle to the outside. It should be

borne in mind, however, that it is not a true fissure, and simply represents an artificial slit made by tearing away that part of the ventricular wall.

The **corpus striatum** is composed of two ganglionic masses of grey matter, an inner and an outer. The inner portion is termed the **nucleus caudatus,** and it projects far into the floor of the anterior cornu of the ventricle as a pear-shaped body with the larger end in front and the hinder smaller end passing backwards into the descending horn. The outer, somewhat smaller part of the corpus is the **nucleus lenticularis,** and the two nuclei are separated

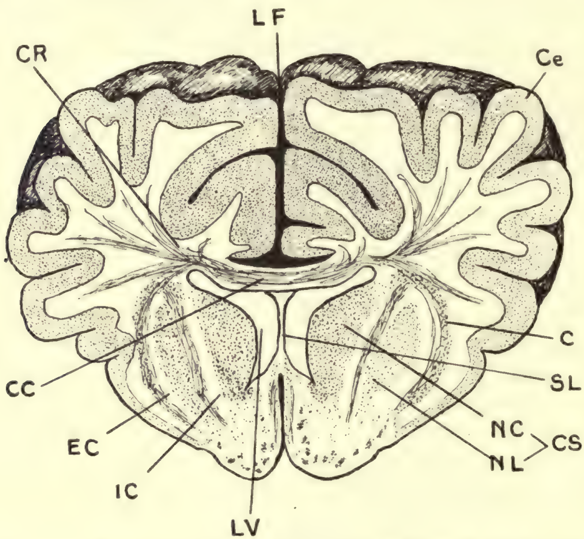


FIG. 120.—Transverse section of cerebral hemispheres in region of corpus striatum.

C., claustrum ; C.C., corpus callosum ; Ce., cerebral cortex ; C.R., corona radiata ; C.S., corpus striatum ; E.C., external capsule ; I.C., internal capsule ; L.F., longitudinal fissure ; L.V., lateral ventricle ; N.C., nucleus caudatus ; N.L., nucleus lenticularis ; S.L., septum lucidum.

by a band of white matter, the **internal capsule,** which passes upwards around the side of the lateral ventricle into the corona radiata. A similar band of white matter, the **external capsule,** runs up on the outside of the lenticular nucleus also to join the corona. Along the outer border of the external capsule is a narrow band of grey matter, the **claustrum.** The **corpus callosum,** as we have seen, is a broad sheet of transversely running white fibres passing from one hemisphere to the other. It continues on into the corona, and thence its fibres are distributed in radiating strands to all parts of the cerebral cortex. At the front end it bends sharply

ventrally and the bend is termed the **genu,** and then passes ventro-posteriorly for a short distance as the somewhat pointed **rostrum.** The hinder end also bends round, but only for a short distance, enlarging to form a blunt mass, the **splenium.** On the lower mesial wall of the ventricle, separated from the corpus callosum by the septum lucidum, is the **fornix.** This is an elongated triangular band of fibres lying in the middle line. Anteriorly it passes downwards and bifurcates to give rise to two small but distinct rounded cords of white tissue which pass downwards and backwards in the walls of the third ventricle to terminate in the corpus mammilare. These are known as the **columnæ fornicis** or **anterior pillars** of the fornix. At the hinder end it reaches back to the splenium of the corpus callosum, and there bifurcates into two coıds, the **posterior pillars** of the fornix or **cruræ fornicis posterior,** which pass along the front or concave margins of the hippocampi as the **fimbriæ hippocampi.** The main mass of the fornix is composed of fibres running in a longitudinal direction, but at the hinder end, connected with the posterior pillars, there is a band of transversely running fibres which serve to form a means of communication between the two hippocampi. These constitute the **hippocampal commissure** or **psalterium.**

The **hippocampus** itself is a large crescent-shaped mass of grey matter which starts as a narrow band on each side just behind the psalterium. It increases rapidly in size and passes ventrally, first posteriorly, then laterally and finally anteriorly, reaching its maximum size in its transverse or lateral portion and narrowing again as it runs forwards. Thus it takes part in the formation of the mesial, posterior and latero-ventral wall of the descending cornu. As already noted, the fibres of the posterior horn of the fornix are closely attached to its anterior concave border as the fimbriæ.

Before leaving the cerebral hemispheres we must consider how they are connected together. The nerve cells of the cortex of the two sides are put in communication with one another by three different transversely running bands of fibres which are called the **cerebral commissures.** Two of these we have already noted, viz. the corpus callosum and the posterior region of the fornix. The third is a small compact band of fibres known as the **anterior commissure,** situated at the front end of the third ventricle. In saggittal section it appears as a circular area just below the anterior end of the fornix, whose anterior pillars pass one on each side of it. If this cord be traced by scraping away the ventrally lying grey matter it will be seen to be horse-shoe shaped, its transverse portion lying just above and partly in front of the optic chiasma. and its two ends passing outwards and forwards to terminate in the olfactory bulbs. A

few of its fibres also appear to run to the frontal and temporal lobes. These three commissures are generally regarded as arising from the **lamina terminalis** or median anterior wall of the embryonic fore-brain. If this be so, then the septum lucidum must be regarded as the attenuated portion of the lamina lying between the corpus callosum and the fornix. All these structures are somewhat displaced from their original position owing to the enormous development of the outgrowths from the antero-lateral parts of the fore-brain to form the cerebral hemispheres.

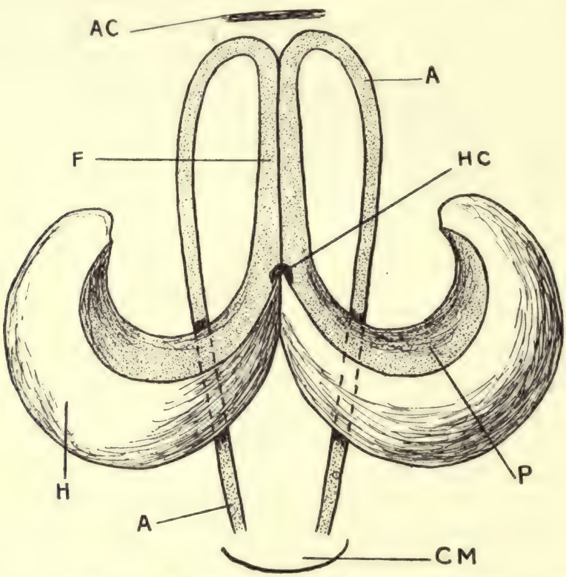


FIG. 121.—Diagram to show relation of fornix and hippocampus, the structures being represented as pulled out laterally.

A., anterior pillar of fornix ; A.C., anterior commissure ; C.M., corpus mammillare ; F., body of fornix ; H., hippocampus ; H.C., hippocampal commissure, psalterium ; P., posterior pillar of fornix, fimbria.

It will be seen then that we can regard the hemisphere as composed of an anterior basal mass, the corpus striatum, joined on to the main stem of the whole brain and a wall that passes from this outwards, backwards, upwards and inwards to enclose the ventricle, and so forming a sort of fold termed the mantle or **pallium.** In this pallium two functionally distinct regions can be distinguished. The first is the ventro-lateral portion, limited externally by the rhinal fissure and hippocampal fissure, and comprising the olfactory bulbs, the pyriform lobes, olfactory tubercles, hippocampi and the fornix. All of this is concerned in the main with olfactory sensations,

and perhaps also with taste. This portion is designated the **olfactory pallium** or **archi-pallium.** In lower vertebrates, for example *Scyllium* and *Rana*, the archi-pallium forms practically the entire bulk of the fore-brain. As we have seen in the mammal, that is the higher mammal, the remaining part of the pallium, lateral, dorsal and dorsal-mesial in position is even larger than the other. Since it is the part that has been added to the old olfactory pallium during the course of evolution, and is particularly characteristic of the latest group, the Mammalia, it is termed the **neo-pallium.** It is very highly developed and concerned with visual, auditory and general body sensations, and the voluntary actions connected therewith. It is also the seat of the higher mental processes, and in man is the seat of the mind. These various activities are not diffused generally through the neo-pallial cortex, but are more or less definitely localised in certain definite regions, the so-called **sensory areas.** For example, along the dorsal region of the hemisphere from before backwards, we find areas for the larynx, face, arm, trunk, leg, tail and anus. On the lateral surface are distinct areas concerned with mastication, oculo-motor and auris centres, and in man there is a speech centre and other regions concerned with association and correlation. To this highly-specialised neo-pallial cortex the mammal owes its great mental powers, which, as has been pointed out, are in the main responsible for its dominating position, and this development and differentiation reach their highest point in man himself.

The third ventricle is a deep vertical cleft lying in the thalamencephalon, and so being the modified embryonic fore-brain vesicle. It is bounded at the front end by the anterior pillars of the fornix and the lamina terminalis, including the anterior commissure and the posterior portion of the septum lucidum. On each side of the latter are the foramina interventricularia, putting the third ventricle in communication with the lateral ventricles. Posteriorly it is much reduced and continued backwards as the iter. The side walls are furnished by the optic thalami. Its floor is formed by the optic chiasma, the tuber cinereum, the corpus mammillare and the part of grey matter of the posterior perforated spot. The roof is very thin, being composed of ependymal epithelium, and immediately above it a double fold of vascular pia mater runs forward some distance under the hinder ends of the hemispheres as the **velum interpositum.** This fold of the pia mater pushes the roof down on the two sides to form the anterior choroid plexuses, which thus project into the ventricular cavity. Anteriorly these plexuses become continuous through the interventricular foramina with those of the lateral ventricles. At each side of the middle line, the

hinder end of the roof and top part of the side wall of the ventricle are thickened to form the **trigonum habenula** or **habenular ganglia.** Between these arises the **pineal body** or **epiphysis cerebri,** a median unpaired outgrowth consisting of a flattened stalk and an enlarged terminal portion. The cavity of the third ventricle projects a short distance into the stalk as the **pineal recess,** and so divides it into **anterior** and **posterior laminæ.** In the anterior lamina runs a transverse band of fibres which connect together the two habenular ganglia, and is known as the **habenular** or **superior commissure.** At the hinder end of the posterior lamina where it passes on into a band of tissue lying between the anterior corpora quadrigemina is another transverse band, the **posterior commissure,** which is functionally related to the optic centres, but anatomically considered as marking the posterior limit of the third ventricle and, consequently, the thalamencephalon. The pineal body itself is a small reddish pear-shaped mass whose functional significance is not clearly understood, and it should really be considered as forming with the structures immediately surrounding it one pineal complex. In the primitive vertebrate this complex has two potentialities, one glandular and one related to vision, so that in some of the lower vertebrates, *e.g.* certain Lizards and the Lampreys, we find it represented by a pair of eyelike structures, the pineal eyes. In other vertebrates such as the mammals, this visual potentiality is suppressed, and the glandular function becomes more marked so that in the adult rabbit and sheep, for example, we find that the single pineal body has apparently a glandular significance.

The **optic thalami** are two large masses of grey matter forming the main part of the walls of the thalamencephalon. They run forward to the corpora striata, from which, however, they are separated by a slight groove, and at the hinder end each terminates in a swelling, the **pulvinar.** They are so thick that they almost obliterate the cavity of the ventricle, and, indeed, in the centre they actually meet and adhere in the middle line over an area known as the **massa intermedia.** This is sometimes referred to as the " middle or grey commissure," an erroneous term, since there is no crossing of fibres at this point, but merely an adhesion. Just behind and slightly lateral to the pulvinar are two ganglionic masses, the **internal** and **external geniculate bodies.** The optic chiasma is formed by a large band of fibres from each side running together in the middle line, some of them pass out away from the brain as the optic nerve of the same side, while others cross over and leave the brain with the optic nerve of the other side. The **optic tract,** as this broad band of fibres is called, passes externally over the lateral surface of the thalamus and terminates in connection with the pulvinar, the external

geniculate body and the anterior quadrigeminal bodies. Certain parts of the lamina terminalis, namely, the anterior commissure, the septum lucidum, the fornix and the corpus callosum, we have already considered ; but there still remains a small, almost unaltered portion of it at the anterior end of the ventricle. This runs from the anterior commissure downwards and backwards to the optic chiasma, and to this the term lamina terminalis in the limited sense may be applied. The chiasma projects into the floor of the ventricle, leaving a small **pre-optic** recess in front of it, whose floor is formed by the lamina. The remaining structures in the floor of the third ventricle have already been considered.

Mid-Brain.

The mid-brain occupies but a small part of the total brain mass in the adult and its cavity, the **iter a tertio ad quartum ventriculum** or **aqueduct of Sylvius,** is reduced to a short narrow passage which is roofed by the quadrigeminal bodies and has its side walls formed by the crura cerebri. The **anterior quadrigeminal bodies** or **colliculi superiores** are fairly large oval masses, and much larger than the posterior. Each gives off two white bands of fibres, an **anterior brachium,** which passes forwards and downwards behind the pulvinar into the optic tract, and a **posterior brachium**, which passes down to disappear under the internal geniculate body. The **posterior quadrigeminal bodies** or **colliculi inferiores** are small structures underlying the former, and each gives off a small brachium which can be traced forward to the posterior part of the corona radiata.

The **crura** or **pedunculi cerebri** are two large masses running backwards from under the hemispheres and coming out between the hippocampal lobules. They pass backwards from the optic chiasma, visible on the ventral surface as two wide pillars, and leaving between their anterior ends the posterior perforated spot, and they disappear beneath the pons. As noted, they are extremely thick, and constitute the side walls and floor of the iter.

Hind-Brain.

The visible dorsal surface of the hind-brain is composed entirely of the cerebellum. In the middle line this is constituted by a median longitudinal portion termed the **vermis**, the surface of which is marked by a number of close-set transverse sulci. At its lateral border is a longitudinal fissure separating it from the lateral lobe of the cerebellum, or **hemisphærium cerebelli.** This in its turn has attached to its ventro-lateral border a small lateral lobe, the

flocculus, traversed only by five or six sulci. Between the flocculus and the hemisphærium is a lateral lobe, the **paraflocculus,** bent upon itself and covering the dorsal surface of the flocculus.

The antero-ventral surface is marked by a broad, slightly raised transverse band of tissue, the **pons Varolii,** whose sides pass round latero-dorsally to join the cerebellum. The two structures, pons and cerebellum, form the major part of the metencephalon. Just behind the pons lies another less conspicuous transverse area, the **corpus trapezoideum,** which is marked in the middle line by a shallow longitudinal groove, the **ventral sulcus,** that passes back to become continuous with the ventral fissure of the spinal cord. It also bears two median longitudinal bands, the **pyramids,** one on each side of the furrow. Behind this again these fairly narrow pyramidal tracts pass backwards, and are obliquely truncated at their posterior extremities, this region being termed the decussation of the pyramids, since at this place fibres from one side of the brain pass over to the opposite side of the spinal cord. From this region onwards the floor of the **medulla oblongata** or myelencephalon passes backwards without noticeable line of demarcation into the spinal cord.

The **fourth ventricle,** the cavity of the hind-brain, is not visible externally, since it is covered by the cerebellum. It is a long triangular depression on the dorsal side of the hind-brain, continuous with the iter in front and the canalis centralis of the spinal cord behind. The ventricular roof is very thin, being formed of ependyma and the overlying pia mater. It is divided into two moieties by the cerebellum. The front part, known as the **anterior medullary velum** or **valve of Vieussens,** runs back from the posterior colliculi under the anterior end of the cerebellum, with which it becomes continuous. It contains a layer of nervous matter, thin posteriorly, but thickening in front. The hinder portion of the ventricle is roofed by the **posterior medullary velum** or **choroid plexus** of the fourth ventricle. This is mainly non-nervous and highly vascular, and it passes forwards under the end of the cerebellum, with which it becomes continuous.

The cerebellum is joined to the rest of the brain on each side by three large bands of white tissue, which help to form the dorso-lateral walls of the ventricle. The most anterior is the **brachium conjunctivum** or **anterior cerebellar peduncle,** which runs downwards and forwards beneath the corpora quadrigemina, and between the two brachia stretches the anterior medullary velum, which becomes fairly thick at its front margin. The **middle cerebellar peduncle** or **brachium pontis** is a stout band of white fibres passing ventrally to form the main mass of the pons, which thus

constitutes a connection between the two hemispheres of the cerebellum. The **posterior** or **inferior peduncle** is constituted by fibres running to the restiform bodies. The cerebellum itself is deeply cut into by the sulci, and the grey matter on its periphery is thrown into a number of subsidiary folds with the result that the white matter presents a very characteristic tree-like appearance in sagittal section, and is for that reason termed the **arbor vitæ.** The side walls of the fourth ventricle are composed to a considerable extent of two large masses, the **areæ acusticæ,** to which the auditory nerves are related. Just behind this and dorso-lateral to it are two transverse masses, the **corpora restiformia.** The floor of the ventricle is mainly composed of a thick mass of grey matter, the **medulla oblongata,** continuous behind with the spinal cord and containing a number of important ganglionic masses related to the nerves arising from it. The positions of some of these are indicated by slight internal elevations.

Origins of Spinal Nerves.

Now that the general anatomy of the brain has been studied it is easy to pass on to consider the points of origin of the cranial nerves.

The **nervus terminalis** is a small nerve with which apparently sympathetic nerves are associated. It originates in the ventromesial wall of the hemisphere ventral and lateral to the olfactory tract and quite close to the lamina terminalis.

The first nerve, or **olfactorius,** is not a single structure, but is represented by numerous small nerve bundles coming in from the olfactory membrane through perforations in the cribriform plate to enter the olfactory bulb. From a small elevation, the accessory olfactory bulb, on the mesial side of the bulb, arise a group of fibres constituting the small **naso-vomerine nerve** or **nervus septalis.**

As we have seen, the second nerve, or **opticus,** coming from the eye, pierces the ventro-lateral cranial wall at the optic foramen and runs inwards and backwards to join the ventral side of the optic chiasma which it helps to form.

The third nerve, the **oculomotorius,** is medium-sized and arises on each side by three or four roots, leaving the crura cerebri near the middle line about half-way between the corpus mammillare and the front border of the pons.

The fourth nerve, the **patheticus** or **trochlearis,** is quite small, and the only one arising from the dorsal surface of the brain. It springs from the dorso-lateral part of the thickened anterior margin of the anterior medullary velum just behind the colliculus inferior. Thence

it passes latero-ventrally, and shows from the ventral surface just in front of and to the side of the pons.

The fifth nerve, the **trigeminus,** is very large and stout, and comes from the ventro-lateral aspect of the pons below the cerebellum. It arises by two roots close together, an external sensory root and an internal smaller motor root.

The sixth nerve, the **abducens,** is quite a small nerve springing from the corpus trapezoideum at the lateral border of the pyramid.

The seventh nerve, the **facialis,** is of moderate size, and emerges from the ventro-lateral border of the corpus trapezoideum slightly behind the level of the fifth nerve.

The eighth nerve, the **auditorius,** is about the same size as the preceding, and arises just external to it. The main trunk almost at once breaks into two branches, the **cochlear** and the **vestibular,** which pass parallel with the seventh to the meatus auditorius internus and are distributed to the correspondingly named part of the labyrinth.

The ninth, or **glosso-pharyngeus** nerve, has three roots, and the tenth, or **vagus,** arises by four roots. These all arise behind one another on the latero-ventral border of the front end of the medulla, slightly medial to the seventh and eighth, and the foremost root comes off just behind the corpus trapezoideum.

The eleventh, or **nervus accessorius,** arises by about ten thin roots, and the most posterior of them is well down the spinal cord at about the level of the fifth spinal nerve. The posterior end of it runs forward along the side of the anterior end of the spinal cord, entering the cranium through the foramen magnum. It leaves the cranium through the foramen lacerum posterium in company with the ninth and tenth nerves.

The twelfth nerve, the **hypoglossus,** takes origin from eight or nine fine roots from the hinder end of the medulla, nearer the middle line than the ninth or tenth and slightly behind the latter. The foremost roots come from the lateral border of the pyramids, and consequently certain of them are on the same level as some of those of the accessories, but mesial to them.

Thus it will be seen that although in conformity with long-established custom we still speak of twelve cranial nerves in mammals, there are in reality fourteen, the two extra ones being the nervus terminalis and the nervus vomeronasalis or septalis, as noted previously.

CHAPTER XIV

HISTOLOGY AND CYTOLOGY

In the foregoing pages we have seen that the body of a higher animal consists of a supporting skeleton, the flesh, and a large number of **organs** arranged in **systems** ; we can even speak of the skeletal and muscular systems regarding the individual parts as organs. Generally speaking, each of these organs is of a characteristic shape, and always, when examined in greater detail, is seen to be composed of a definite **tissue,** as it is termed, or a combination of tissues. When we proceed still further we find that many of these tissues are composed of small units, termed **cells,** and when we take into account their development we find that all parts of the body are composed of cells or of structures formed by or from cells. This statement of the composition of the body of the higher animals is sometimes termed the "**cell theory,**" and while it is possible to indicate certain exceptions, it may be taken to be in the main a true one. We thus have two special branches of minute anatomy, and also of physiology, since we can also discuss them from the point of view of function, namely, "**Histology,**" the study of the tissues, and "**Cytology,**" the study of the cell. Certain general points regarding each of these need considering.

Histology.

The actual details of the histology of a number of different tissues have already been dealt with in treating the different animal types, and it now only remains to indicate the way in which these tissues may be classified for the purposes of study. In the first place we may regard them from the point of view of similarity of structure and function, and we find that they can be separated into four main groups : (1) Epithelial, (2) Connective, (3) Muscular, and (4) Nervous tissue. In addition to these are the two body fluids, the blood and the lymph, which, since they contain cells, may be conveniently treated with the tissues, and, indeed, are regarded by some authorities as being highly specialised connective tissue.

An **epithelium** is a layer of cells covering free surface ; it need not

be an external surface, for it can line an internal cavity. Epithelia may be divided in the following way.

Simple epithelia consist of but one layer of cells, and are subdivided according to the shape of the cells into: **Squamous,** consisting of flat cells; **Cubical,** in which the cells are approximately cubical in shape; and **Columnar,** with cells much longer than they are wide.

Compound epithelia have their cells arranged in a number of superimposed layers, and are subdivided into: **Stratified,** in which the cells are arranged in a series of layers, the innermost cubical or polygonal, and the outermost quite flat. This is the most common and typical, and **Transitional,** consisting of two or three layers, all of more or less polygonal cells, and not becoming flattened on the outside. This latter variety is found in the bladder and the cornea of the eye.

It is the epithelia, particularly the simple ones, that provide most of the secretory tissues of the glands, and, consequently, we find that almost any type of epithelium may be glandular in nature. They also form the essential part of the sense organs, where they are termed **neuro-epithelia.** A further modification is to be found in the pharyngeal region of *Rana,* and in the trachea of *Lepus,* where the cells are provided with an external covering of cilia constituting a **ciliated epithelium.**

As a rule, we find that the glandular epithelium does not remain upon the surface, but becomes invaginated to form a gland. This may be a simple ingrowth, and so form a **tubular gland,** such as we find in the mucosa of the stomach, or, if its deeper end or fundus is much enlarged, it produces a **flask** or **saccular gland,** similar to those in the skin of *Rana.* On the other hand, the invagination may become complexly branched and, if its branches remain tubular, form a **compound tubular gland,** as in the kidney, or, if the ends of the branches dilate, a **compound saccular** or **racemose gland,** as in the pancreas and salivary glands.

The **connective tissues,** as we have seen, are characterised by possessing a fluid matrix in which their cells float, and through which pass typically white and yellow fibres. Any one of these elements may be modified, developed to a marked degree, or, on the other hand, suppressed. In certain cases also, as in adipose tissue, bone, etc., other substances may be laid down in it. The various kinds of tissue included under the heading of connective tissues are: Areolar or Sub-cutaneous, Fibrous, Elastic, Adipose and Lymphoid tissues, and Bone and Cartilage. By some authorities Blood and Lymph are also regarded as being highly specialised varieties of connective tissue.

The **muscular tissues,** as we have seen, are of two kinds, exhibiting a fundamental difference. In the first place we have the varieties in which the cellular structure is retained as in the involuntary and cardiac muscle. In the second place there is the voluntary muscular tissue which, while commencing in the embryo as strands of mesodermal cells, ends as long complicated fibres without any trace of cellular structure, but in the formation of each of which a number of cells took part. All muscular tissue is characterised by exhibiting the power of contractility to a marked degree.

The **nervous tissue** is composed of highly modified and very characteristic cellular elements, the neurons, and much of the total bulk of the nervous tissue in the body is constituted by the processes of these cells and the protective medullary sheath they have developed around them.

There is, however, another and entirely different way of classifying the body tissues in animals, and that is according to their derivation. As we shall see later, at a very early stage in the development of the embryo of all higher forms we can recognise three layers of cells, namely, an **ectoderm,** covering the outer surface ; an **entoderm,** forming the lining of the main part of the gut from pharynx to rectum ; and a **mesoderm,** which lies between these two layers. Within the mesoderm a cavity, the cœlom, appears, so that it becomes divided into two layers, an outer part helping to form the body wall, and an inner part taking part in the formation of the gut wall, but both, of course, are just parts of one and the same layer. Through the presence of the cœlom, however, it is possible to recognise quite early two parts of the mesoderm that have slightly different fates. The layer lining the cœlom is by its very position an epithelium, and is spoken of as the **mesothelium** ; while the remaining part between this and either the ectoderm or entoderm is in the embryo a sort of non-specialised padding tissue, and so termed the **mesenchyme.** The result is then, that we can divide up the tissues of the adult into three main groups, according to the embryonic layer from which they are derived, and one of these, that of the mesoderm, falls into two sub-groups :—See over.

This classification, while not of much assistance in practical work in histology, since it is not based on structural similarity, is of considerable importance in comparative work, and also in a consideration of the nature of the organ and of the diseased or pathological conditions to which it may be subject.

CLASSIFICATION OF THE TISSUES.

A. ECTODERMAL.

1. Epidermis:
   (*a*) Epidermal appendages, hair, scales, etc.
   (*b*) Skin glands (sweat, sebaceous, mammary, lachrymal).

2. Epithelium of:
   (*a*) Conjunctiva.
   (*b*) Olfactory chamber (neuro-epithelium).
   (*c*) Auditory organ (neuro-epithelium).
   (*d*) Oral cavity, oral organ, enamel organ, salivary glands, part of hypophysis.
   (*e*) Anus, rectal glands.
   (*f*) Chorion.
   (*g*) Amnion.
   (*h*) Lens.

3. Nervous tissue.
   (*a*) Cells of brain, spinal cord and sympathetic ganglia.
   (*b*) Retina of eye.
   (*c*) Ependymal epithelium.
   (*d*) Part of hypophysis.
   (*e*) Pineal body.

B. MESODERMAL.

1. Mesothelium:
   (*a*) Epithelium of pericardium, peritoneum, pleura, urogenital organs and kidney.
   (*b*) Striated muscles.

2. Mesenchyme:
   (*a*) Connective tissue, non-striate muscle, adipose tissue, and pigment cells.
   (*b*) Supporting tissue, cartilage, bone, ligament, bone marrow.
   (*c*) Spleen.
   (*d*) Blood, blood-vessels, endothelium.
   (*e*) Eye-parts except lens, retina, and conjunctiva.
   (*f*) Framework of gonads.

C. ENTODERMAL.

1. Notochord.

2. Epithelium of:
   (*a*) Digestive canal, glands (gastric, intestinal, liver and pancreas), allantois.
   (*b*) Pharynx, Eustachian tubes, tonsils, thymus, thyroid.
   (*c*) Respiratory tract, larynx, trachea, lungs.

Cytology.

As we have seen, when we study the details of any tissue we are brought down to the cell as the ultimate particle in almost all cases. The cells are the fundamental vital units, and, indeed, in some cases, *e.g.* the corpuscles of the blood and lymph, appear to be almost separate organisms, only dependent on the body to a certain extent. Just as the cell can be regarded as the structural unit, so it must also be looked upon as the physiological unit, for all questions of function ultimately can become questions of the physical and chemical changes occurring in the cell. In the case of the lowest animals, the Protozoa, the cell is in all senses the living unit, for each cell constitutes a separate individual capable of manifesting all the vital phenomena. As we ascend the animal scale, however, we find, in the cell aggregates we call the Metazoa, that the capabilities of individual cells become limited, and we have a division of labour brought about whereby certain functions are confined to certain

groups of cells. *Pari passu* with this gradual division of function as we ascend the animal scale we find also a gradual differentiation of structure whereby the cells originally equipotential, or approximately so, and of similar structure, become totally unlike and particularly fitted for different purposes. In the course of our examination of the higher types we have noted numerous illustrations of the differential specialisation of structure, and we have seen, for example, how nerve cells, bone cells, glandular cells, muscles, and so on, are quite different from one another, and each adapted to perform its own work. However much they have been changed, however, with few exceptions, they still remain cells, and we may now consider the structure of an idealised cell from which they can all be derived. Naturally this will be far more like the primitive Protozoon than the cell of any tissue of a higher form with the exception of the white blood corpuscles and the lymph cells, which are not much specialised.

The cell consists of a more or less independent mass of protoplasm within which is a denser body, the nucleus, so that we are able to distinguish a cell body composed of **cytoplasm,** and the inner part the nucleus, the material of which is often termed **nucleoplasm.** Under the low powers of the microscope this protoplasm appears as a granular, semi-transparent, greyish-white mass of very viscous substance, and under higher magnification it is seen to present a very characteristic reticulate appearance, which has been interpreted in different ways by various authorities. It was supposed that protoplasm is composed of a sort of sponge-like interlacing network of solid fibres, termed the **spongioplasm,** the interstices of which are filled with a fluid substance, the **cell sap** or **hyaloplasm.** There are certain objections from the physical aspect to this way of looking at things, and while the terms have been retained here as convenient for descriptive purposes, it is not intended to imply that the theory with which they are associated is the correct one ; indeed, it has been almost completely given up. The most generally accepted explanation is that protoplasm possesses an emulsion or foam-like structure resulting from the mixture of substances of different surface tensions, and that the so-called fibres composing the spongioplasm are probably produced by the different optical properties of the constituents, and that this appearance is retained permanently when the protoplasm is killed. It is possible that actual condition varies with the different stages of physiological activity of the cell. When dealing with so small, delicate and transparent an object as the living cell it is extremely difficult to make out its finer structure accurately without staining it in some way to emphasise its components. This procedure usually necessitates killing the cell in some

way, so that actually our knowledge of most of its details is obtained from a study of the dead cell. One of the first objects of Cytology, therefore, is to devise ways of killing the cell in such a manner that its structure remains as much like the living cell as possible. This process is termed **fixation,** and a number of different solutions have been discovered for fixing cells and tissues. Each of these acts most favourably with certain kinds of cells, or shows up certain

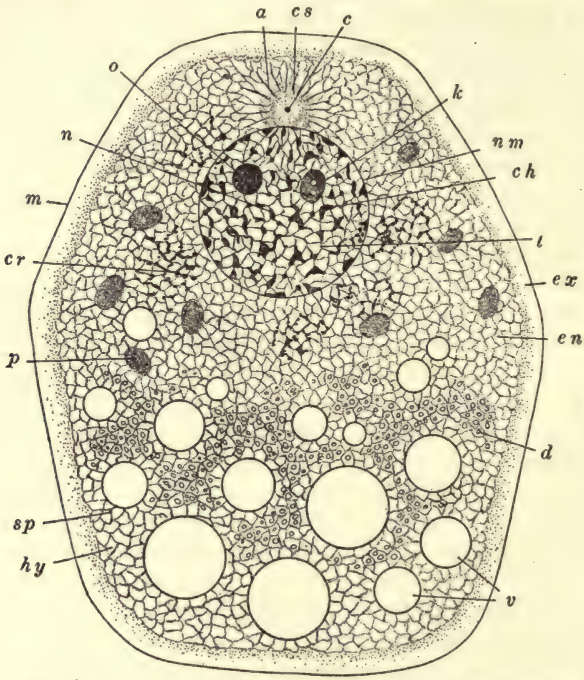


FIG. 122.—Diagram of a typical cell.—From Kellicott.

a., aster *c.*, centrosome (centriole) ; *ch.*, chromatin ; *cr.*, chromidia ; *cs.*, centrosphere ; *d.*, deutoplasmic granules ; *en.*, endoplasm ; *ex.*, exoplasm (cortical plasm) ; *hy.*, hyaloplasm ; *k.*, karyosome ; *l.*, lining network ; *m.*, cell membrane ; *n.*, nucleus ; *nm.*, nuclear membrane ; *o.*, nucleolus ; *p.*, plastids ; *sp.*, spongioplasm ; *v.*, fluid vacuoles (metaplasm).

structures in the cell, or is specially adapted for use when it is to be followed by certain staining substances ; and although some have a much wider range of action than others, not one is the best for use under all or any circumstances. It is beyond the scope of an elementary book to go further into this important matter, but it should be borne in mind that, in the description that follows, various methods of treatment are necessary in order to render conspicuous all the structures considered.

Under the high powers of the microscope it will be seen that protoplasm, in addition to showing the structure just noted, always presents a granular appearance. This is due to its containing a number of tiny particles that in fixed cells appear as solid granules, and are of several different kinds. In the first place there are always present an enormous number of minute granules, the **microsomes,** which are distributed along the spongioplasm fibres, and appear to be an essential constituent of the protoplasm. The cells of the lower animals, particularly the Protozoa, often have granules of an easily staining material—**chromatin,** which is really, as we shall see later, a constituent of the nucleus that has wandered out into the cytoplasm. These **chromidia,** as they are termed, are not common in the cells of the higher animals. Then, too, we have a number of slightly larger granules not necessarily related to the spongioplasm that are the result of the chemical activity of the cell, and may represent food material, which is stored as a reserve or, as the result of the anabolic changes, is on the way to being transformed into protoplasm ; or, on the other hand, they are the katabolic products of the cell going to form its secretions or waste matter. These are included in the general term **metaplasmic granules.** In many cells, more particularly the germ cells, are yet other groups of somewhat larger bodies that may be of a spherical shape, when they are termed **chrondosomes,** or of an elongated or rod shape, termed **mitochondria.** They can easily be seen after certain methods of fixing and staining, but disappear after other fixing fluids. Different varieties of these bodies have been made out, and the terminology employed to describe them is not uniform, and sometimes contradictory ; but for elementary purposes it is sufficient to note their presence, and that they can perhaps be included under the terms given. Their exact significance has not yet been ascertained, but it has been shown that they play an important part in the activities of the cell, and when the cell divides they appear to be more or less carefully distributed to the daughter cells. In many cells we find certain spaces filled with a clear fluid and termed **vacuoles.** In the case of free-living cells these often represent the digestive or excretory apparatus, as we have seen in the case of *Amœba* and *Paramœcium.* Certain cells also contain cytoplasmic specialisations, to which we can give the general name of **plastids.** They are most frequently met with in plant cells, and are the centres at which some substance is collected, *e.g.* the chloroplasts containing the chlorophyll, or the amyloplasts where the starch is aggregated.

There is also, in the cytoplasm, another compound structure situated quite close to the nucleus, and, indeed, the evidence provided by certain Protozoa seems to show that primitively it was

actually a part of the nucleus itself, within which it is to be found in some forms. In the cells of higher animals, however, it lies outside the nucleus, and so can be considered as a cytoplasmic inclusion. It takes the form of a tiny spherical granule, termed the **centriole** or **centrosome,** that stains very intensely with certain dyes and so stands out quite clearly. Often in higher forms it is not single, but a pair of granules side by side, and it is then termed the **diplosome.** Strangely enough this granule, so constant in animal cells and, as we shall see later, playing such a notable part in the process of cell division, has not been shown to be present in plant cells, and so its presence constitutes one of the most striking and, up to now, inexplicable differences between the cells of animals and plants. It is surrounded by a small sphere of very clear, apparently structureless protoplasm, spoken of as **archoplasm,** while the sphere itself is termed the **centrosphere** or **attraction sphere.** This, then, completes the list of the main structures to be found in the cytoplasm.

The nucleus in the higher animals is in the form of a sphere or a more or less elongated ovoid, but in the Protozoa it may be of a very irregular shape, and in some cases divided up into two parts of different functions. The nucleus, as a whole, plays a very important part in the activities of the cell, and appears to be the controlling centre of the cell. Not only does it seem responsible for the chemical changes in the cytoplasm, particularly those leading to assimilation, but it also takes the initiative in the processes leading up to cell division.

The most important constituent of the nucleus is a material termed chromatin, which is generally distributed throughout the nucleus in the form of granules and threads. In lower animals some of it may be extranuclear in position. It receives its name from the fact that it very readily takes up certain basic dyes, such, for example, as hæmatoxylin. Its full significance will be more readily appreciated when we come to consider the part it plays in division and in the activities of the germ cells. Chemically, chromatin is noticeable because it contains nucleic acid, an organic acid rich in phosphorus. Another important part of the nucleus is the **linin** or **achromatin,** so called because of the difficulty with which it can be induced to take up stains. This is in the form of a fine interlacing network of fine fibres with which the chromatin is closely associated. The nucleus is separated off from the cytoplasm by a very thin, homogeneous **nuclear membrane,** which also seems to be made of the same achromatinic substance and is difficult to stain.

Two other substances are present in the nucleus which also stain readily and very similarly to chromatin. The first of these is **volutin,** which with special treatment stains slightly differently from

chromatin, and is regarded as forming a reserve from which the chromatin is recuperated as it is used up. The other is termed **plastin,** and this is harder to differentiate by means of staining, but it behaves differently during division. Within the nucleus is usually one or several distinct rounded bodies that may be of two different kinds. The **nucleolus** is a rounded mass of plastin and takes no part in division. The **karyosome** appears to consist of a plastin basis with which is incorporated a greater or less amount of true chromatin, and so it takes part in division.

Lastly, we have the fluid portion of the nucleus which appears to be somewhat more liquid than that of the general cytoplasm, and is termed the **nuclear sap** or **enchylema.**

Having considered the structure of the cell and the nucleus, in what is termed the resting condition, we can examine the manner in which it divides. It has been noted that reproduction in the Protozoa is brought about by cell division, and that the multicellular condition of the Metazoa results from the same process, only the daughter cells as they are produced do not separate, but remain together to form layers. Two distinct kinds of cell division occur, but both of them agree in that it is the nucleus that initiates the activities, and that the cytoplasm follows. The first method is the simplest, and is known as **direct division** or **amitosis,** in order to contrast it with the second variety, which is termed **indirect division, mitosis** or **karyokinesis.**

The first indication of direct division is the elongation of the nucleus, which is followed by a lengthening of the cell in the same plane. The nucleus then becomes dumbbell-shaped and finally breaks into two, one part going to each end of the cell. Shortly after this a constriction appears in the middle of the cell, which gradually deepens and finally divides it into two, each of which contains a nucleus. Although a simple form of division, it is a comparatively rare one. It occurs, as we have seen, in the macronucleus of *Paramœcium,* possibly in some forms of *Amœba* and in the higher animals in certain pathological conditions, such as cancerous growths.

Indirect or **mitotic division** is more complicated, and its details vary slightly in different animals ; but there is a sufficient general resemblance to enable us, for descriptive purposes, to divide the process into four more or less distinct stages, namely, the **prophase,** the **metaphase,** the **anaphase** and the **telophase.**

The first indication of the approaching division is given by the centrosome, which, if single, divides into two granules that move apart, or, if double already, they start to separate. When they have moved about a short distance each is surrounded by a series of

radiating lines, the **astral rays,** and is termed an **aster.** During this time the chromatin of the nucleus becomes more in amount and stains more readily, and it takes up its position on the linin threads apparently as a series of granules. The karyosome breaks up and contributes its chromatin to the general supply, while the nucleolus is apparently passed out into the cytoplasm, where it disappears, taking no part in the subsequent changes. All the chromatin becomes arranged in a long convoluted and seemingly continuous thread, termed the **skein** or **spireme.** The asters separate more widely, and as they do so their adjoining fibres unite to form a long spindle-shaped arrangement termed the **spindle.** The centrosomes pass on until they come to lie at opposite poles of the nucleus, through which the spindle fibres are enabled to pass because of the disappearance of the nuclear membrane. Meanwhile, the spireme becomes broken up into a number of definite independent pieces, usually about equal in length, termed the **chromosomes,** which finally take up a fairly symmetrical position in the middle of the spindle, with their length at right angles to the line joining the centrosomes, and form what is termed the **equatorial plate.** Thus is produced a very characteristic arrangement; there is a centrosome at each end with its radiating astral rays, and, joining them, the spindle, now strongly marked and quite wide in its middle region. Across the widest part is arranged the equatorial plate of chromosomes, which are situated in the peripheral region of the spindle. The outermost spindle fibres seem to be attached to the chromosomes, and so form, as it were, an outer zone, sometimes described as the **mantle fibres,** surrounding the inner central core of the spindle, the fibres of which pass from one end to the other. This completes the typical **prophase,** and the resulting figure is a very striking one and known as the **amphiaster** or **achromatic figure.**

While a certain amount of variation is met with, for example, the entire spindle may be well formed outside the nucleus, and later, as it were, break across it; yet we find in general a fairly close similarity in the prophase, as it is found in practically all species of higher animals. Among some of the Protozoa we can see certain marked differences, so much so that they suggest that the process of mitosis was evolved in that phylum, and that certain of its members have not yet developed to the stage when its mechanism has been perfected, and in simple cases the whole figure may arise within the nuclear membrane. In the normal divisions of all the cells of the body and its various tissues, in both the embryonic and adult stages, there is produced an amphiaster. As has been pointed out, it appears as if actual fibres are produced, some of which are attached to the chromosomes, and others not, and it may be significant that

their configuration in the amphiaster resembles quite closely the disposition of the lines of force in an electro-magnetic field. The

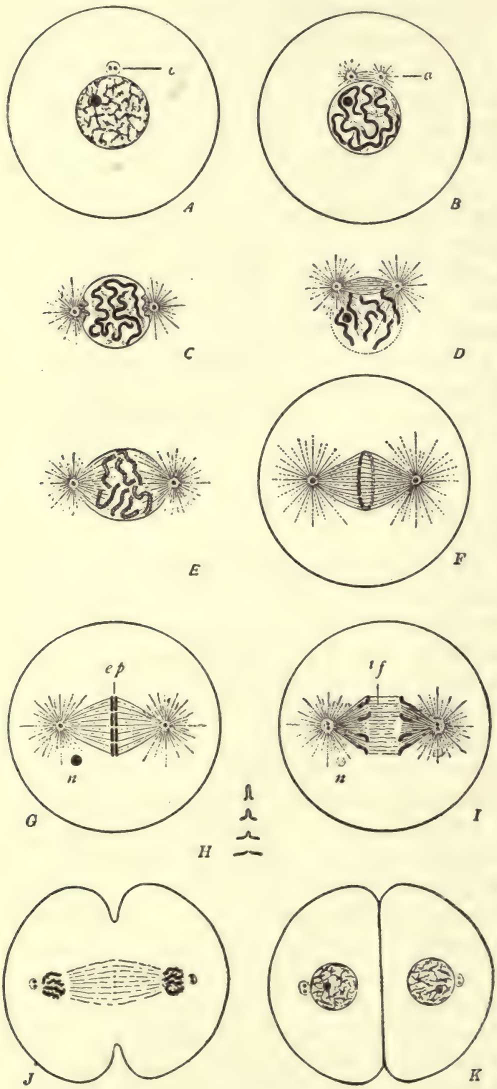


FIG. 123.—Diagrams of the process of mitosis. "Cell" slightly modified.—From Kellicott, after Wilson.

A, resting cell with reticular nucleus and true nucleolus; at *c.* the attraction-sphere containing two centrosomes. B, early prophase; the chromatin forming a continuous "spireme," nucleolus still present; above, the amphiaster (*a*). C, D, two different types of later prophases; C, disappearance of the primary spindle, divergence of the centrosomes to opposite poles of the nucleus (examples, many plant-cells, cleavage-stages of many eggs). D, persistence of the primary spindle (to form in some cases the "central spindle"), fading of the nuclear membrane, ingrowth of the astral rays, segmentation of the spireme-thread to form the chromosomes (examples, epidermal cells of salamander, formation of the polar bodies). E, later prophase of type C; fading of the nuclear membrane at the poles, formation of a new spindle inside the nucleus; precocious splitting of the chromosomes (the latter not characteristic of this type alone). F, the mitotic figure established. G, metaphase; splitting of the chromosomes (*e.p.*); *n.*, the cast-off nucleolus. H, four stages in the divergence of the two halves of a chromosome. I, anaphase; the daughter-chromosomes diverging, between them the interzonal fibres (*i.f.*), or central spindle; centrosomes already doubled in anticipation of the ensuing division. J, late anaphase or telophase, showing division of the cell-body, mid-body at the equator of the spindle and beginning reconstruction of the daughter-nuclei. K, division completed.

actual nature of these threads, *e.g.* whether they are threads or an arrangement of the nucleoplasmic structure, and so on, is not quite

clear, and there are conflicting theories put forward as to the forces that are responsible for the phenomenon.

The chromosomes themselves take on a variety of forms, spheres, short rods, long rods, V-shapes, Y-shapes, and so on, and different-shaped chromosomes may occur in one and the same nucleus, though each species or tissue usually retains the same arrangement in its mitoses. The next step in the division, *i.e.* the **metaphase,** is that each individual chromosome splits longitudinally, that is, in a direction at right angles to the long axis of the spindle. Half of each chromosome, therefore, is apparently attached to the mantle fibres of one aster, and the other half to the fibres of the other aster. This constitutes the essential stage in mitosis, and to which the prophase can be considered as preparatory. In the latter we find that the chromatin is collected up, sorted out into definite pieces, the chromosomes, and these are so arranged that their division and distribution can be carried out as accurately as possible. The remaining two phases can be regarded as, in a way, reconstruction and finishing stages, serving to secure the proper distribution of the chromatin. In some instances there is, as it were, a pushing forward of the splitting process, even as far as the spireme stage, so that from that point on the chromatin and chromosomes when formed are double. Strictly speaking, the term "metaphase" can only be applied when the chromosomes split after being arranged in the equatorial plane, but it will be seen that, whatever method may be adopted, it does not alter the fundamental phenomenon of the sorting and division of the chromatin into equal and similar portions.

In the **anaphase** the halves of each chromosome move towards the opposite poles of the amphiaster. It appears as if their rôle in this is entirely a passive one, and that they are drawn apart by the contraction of the mantle fibres. The groups of chromosomes are carried right to the pole, and so are ready for the last stage. As the groups separate there will be left in the middle region of the spindle, the central fibres, which are now termed the **interzonal fibres.** These are further added to by other fibres which appear between the diverging chromosomes in the position formerly occupied by the mantle fibres. The origin of these secondary fibres is not clear, but they are also included in the term "interzonal fibres." In plant cells frequently the interzonal fibres thicken in the middle to form what is known as the mid-body or cell plate, and this appears to take part in the formation of the cell wall separating the daughter cells. During this phase there is usually a definite constriction in the cytoplasm of animal cells, foreshadowing its division into two in a plane passing through the middle of the interzonal fibres.

The concluding stages, the **telophase,** lead to the transformation of

the chromosome groups at the two poles into the condition of the resting nucleus, with its membrane and reticulum restored. This may be regarded as being brought about by a process that is practically the reverse of the changes occurring in the prophase. It is subject to considerable variation, and in the case of rapidly dividing cells, such as we find in developing animals or tissues, may be practically omitted. The centrosome of each nucleus may divide into two during the anaphase, and all that is necessary is for the chromosome group at the end of the anaphase to rotate through an angle of 90° so as to constitute a typical amphiaster practically at once. The stages of the telophase are passed through if the cell returns to a normal non-dividing condition, and the above variations may be regarded simply as short cuts to enable cell division to proceed at a rapid rate. While the nuclear reconstruction is proceeding, or very shortly after it is completed, the cytoplasm of the mother cell is cut into two and two daughter cells are produced.

Certain points in connection with mitosis need to be emphasised. In the first place we see that it is an elaborate mechanism which has as its result the careful collecting up of the chromatin into a number of definite bodies, the chromosomes; each of these is split into two, and a half goes to each daughter cell. Thus not merely is the chromatin content of the nucleus halved in amount, but it is first sorted out and halves of the individual units distributed to the new cells, suggesting that the halving is also qualitative. It would appear from the universality of the occurrence of mitosis and the consistency of its result, that it is necessary for this material to be carefully dealt with, and so apparently the chromatin itself must be of great importance to the subsequent activities of the resulting cells. All other cytological evidence tends to confirm this conception of the functional value of chromatin.

Numerous observations on many species of animals have also revealed the fact that in any one species there is a remarkable constancy in the number and variety of chromosomes produced. Thus for each species there is a fixed number of chromosomes, and they are arranged in a fairly constant manner in all the cell divisions of the body, no matter what organ or tissue they are going to form. This constant number is known as the **somatic** or **diploid number.**

It will be noted that this constant number refers to the cells of the body, and the description of mitosis given is similarly applicable to the somatic cells. A modified form of such cell division is encountered in the history of the germ cells, both male and female, in practically all cases. As a result of this modification we find that the mature germ cells contain only half the number of

chromosomes that is characteristic of the body cells, and this is termed the **reduced** or **haploid number.** The exceptions are found in those animals that produce germ cells that can undergo development without fertilisation ; a form of reproduction termed **parthogenesis.** Thus the number of chromosomes in a germ cell, *i.e.* the haploid number, can be represented in a general way by the constant n, and the number in the body cells, or diploid number, will be therefore $2n$.* The processes undergone in the production of the germ cells differ slightly in the two sexes, and need to be treated separately, although, as will be seen, they are fundamentally the same. Cells destined to give rise only to the germ cells appear at a very early stage in the development of animals, including the higher forms ; these are known as the **primitive germ cells.** They take up a position in the tissue that, with their descendants, will give rise to the gonads, and, after a certain period of multiplication, are termed the **spermatogonia** in the male, and the **oogonia** in the female.

The process in the male resulting in the production of the male gametes is termed **spermatogenesis.** The spermatogonia, together with certain other nutritive or nurse cells, form the lining of the seminiferous tubules of the testes. They have been reproduced from the primitive germ cells by a series of ordinary mitotic divisions, and while in the tubule they grow until they attain a certain size, when they again divide into two by mitosis. One daughter cell, the outer, persists as a parent spermatogonium, which grows to regain its original size and then divides again, and so on. The other, and inner cell, forms a **sperm-mother cell** or **primary spermatocyte.** This cell also grows slightly and then divides to form the **secondary spermatocytes ;** but this division is not an ordinary mitotic one, and its main points need to be considered.

The number of chromosomes entering this cell is, of course, the diploid or somatic number. As the spireme appears it passes into an unusual condition, for its fibres all mass together at one pole of the nucleus near the centrosomes to form a dense clump, such as is not encountered in ordinary division, and this condition is termed the **contraction phase** or **synizesis.** After a time this chromatin knot begins to unravel, and almost as it does so it segments into chromosomes ; but the number of chromosomes produced in this way is only half the ordinary, *i.e.* it is the haploid number. Closer examination shows that each apparent chromosome is really a pair of chromosomes in close apposition, but they are not completely

* There are certain exceptions to this also in the case of animals that possess an extra chromosome in one sex, but this is a point into which it is not necessary to enter.

fused, and a narrow longitudinal slit between them can be made out. This coming together of the chromatin threads just before the formation of the chromosomes is termed **synapsis,** and it constitutes a fundamental difference between this type of cell division and

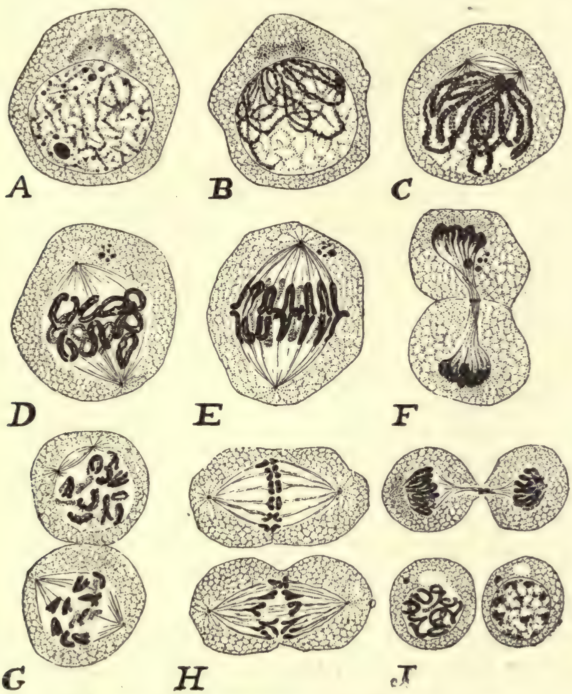


FIG. 124.—Spermatogenesis.—From Bourne.

A, a spermatocyte preparing for the first or meiotic division ; a large karyosome is present and the rest of the chromatin is scattered in the form of granules on the achromatic network of the nucleus ; on the top of the nucleus is the centrosphere with two centrosomes. *B*, spireme with a single row of chromatin granules ; the loops of the spireme show a distinct polarity. *C*, early stage of synapsis, the chromatin granules and the spireme ribbon are divided longitudinally. *D*, twelve *bivalent* chromosomes of various shape becoming arranged round the equator of the spindle. *E*, metaphase of the meiotic division ; each bivalent chromosome is being divided into its two components, one of which is being drawn to each pole of the spindle. *F*, nuclear telophase and first division of the spermatocyte. *G*, two secondary spermatocytes preparing for division ; the upper figure showing an earlier stage of mitosis than the lower ; the nucleus of each spermatocyte contains twelve *univalent* longitudinally-split chromosomes. *H*, the upper spermatocyte shows the metaphase, the lower the early anaphase of the first post-meiotic (homœotype) division. *J*, the two secondary spermatocytes have divided to form four spermatids ; the nuclei are shown in different stages passing from the late anaphase to the resting condition. Note that the figures *G*, *H*, *J* are drawn on a somewhat smaller scale than the rest.

ordinary mitosis, and, as we shall see later, one that is of great importance subsequently. Generally, as these double or **bivalent chromosomes** move to take up their position on the equatorial plate, each of them splits longitudinally and at right angles to the original

cleft. Thus each apparent chromosome consists of four similar pieces lying closely side by side, and in this condition it may be termed a **tetrad.** The division now proceeds as in mitosis, with the result that each daughter chromosome, formed by the separation of the tetrad along the line of the second split, comes to consist of a bivalent chromosome of two pieces side by side. If not already present the second split appears at this stage, and in either case the anaphase is entered upon. Each one of the pair in the bivalent daughter chromosomes is a half of the corresponding member of the pair formed during synapsis.

When this division is watched, therefore, it will be seen that each daughter cell, or secondary spermatocyte, has apparently half the number of chromosomes that went into the original primary spermatocyte. To distinguish this type of division from mitosis it is spoken of as **Meiosis** or **reducing** division. (In older terminology ordinary mitosis was said to be **homœotype,** since each daughter cell had the same number of chromosomes as the parent cell, while meiosis was designated **heterotype,** since parents and daughters did not have the same number of chromosomes.) The subsequent division of the secondary spermatocyte starts in a normal way, and the bivalent chromosomes take up a position on the equatorial plate. Each chromosome is already split, and does not do so again, so that a half goes to each daughter cell or **spermatid.** There is no reduction in the apparent number of chromosomes (in old terminology the division is homœotype), although the chromosomes have become **univalent.**

Thus from each original primary spermatocyte we have produced four daughter cells, each of which contains half the number of chromosomes that went into the primary cell. Moreover, the spermatids only receive half of one member of the bivalent chromosomes formed during synapsis, and not, as might be supposed, a quarter of both. The spermatids, containing the haploid number, undergo no further divisions, but, as the result of an alteration of structure, become transformed into **spermatozoa.**

While the spermatozoa of the higher animals exhibit a variety of shapes and sizes they are composed of essentially the same parts, and the description that follows is based mainly on that of man or one of the higher mammals. Under moderate powers of the microscope a spermatozoon appears to consist of three portions, a small **head,** a smaller **middle piece** or **neck,** and a long fine vibratile **tail.** Further investigations shows that it really possesses a fairly complicated structure, all the parts of which are derived from preexisting portions of the spermatid. The head appears to be mainly composed of the chromatin of the nucleus of the spermatid, and it is

provided at its anterior end with a covering, or **cap,** derived from the centrosphere. This cap serves as an organ for perforating the egg, and is differently shaped in various species. The neck is a very small inconspicuous portion, but important, since it contains granules derived from the centrosome of the spermatid, and from which the centrosomes of the fertilised ovum are presumed to be derived. The tail consists of an axial filament surrounded for the greater part of its length by a cytoplasmic sheath, but three distinct parts can be recognised in it. Firstly, next to the neck is a moderate-sized **connecting piece,** also containing granules derived from the centrosome and other structures; secondly comes a long **main piece** with just the axis and its sheath; and finally an **end piece,** consisting of the axial filament, only without its sheath.

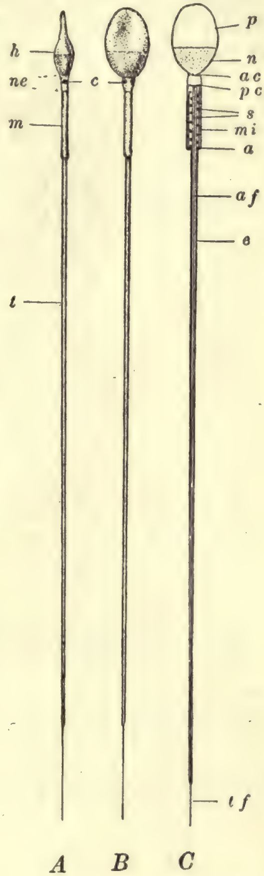


FIG. 125.—Spermatozoa. —From Kellicott.

A, B, two views of a human sperm cell.—After Retzius. × 2000. C, diagram of the structure of a generalised type of flagellate spermatozoon.—After Meves.

a., annulus; *ac*, anterior centrosome; *af*, axial filament; *c.*, centrosomes (end knobs); *e.*, protoplasmic envelope; *h.*, head; *m.*, middle piece; *mi.*, mitochondria; *n.*, nucleus; *ne.*, neck; *p.*, perforatorium (acrosome); *pc*, posterior centrosome; *s.*, spiral filament; *t.*, tail piece; *tf*, terminal filament.

The process of egg formation, or **oögenesis,** in the female, while it differs from spermatogenesis in certain points, is nevertheless fundamentally the same as far as the divisions are concerned. It has not been worked out in so many forms as has spermatogenesis, since the ovum, being loaded with yolk in the lower forms, and being inaccessible in the higher animals, presents greater technical difficulties in investigation. Where it has been studied it has been found to correspond with sperm formation in nuclear detail.

The primitive germ cells undergo mitotic divisions until they are quite numerous, and then follows a period of growth at the end of which they are **oögonia.** Each oögonium divides to produce the **primary oöcytes,** or **ovarian ova,** which are provided with the diploid number of chromosomes by a mitotic division. These then grow until in most forms they are considerably

larger than the spermatocytes, and, indeed, in animals with heavily yolked eggs, may become hundreds of times larger. They then enter into a mitotic division; the spireme concentrates in synizesis, and from the chromatin mass reappear threads that

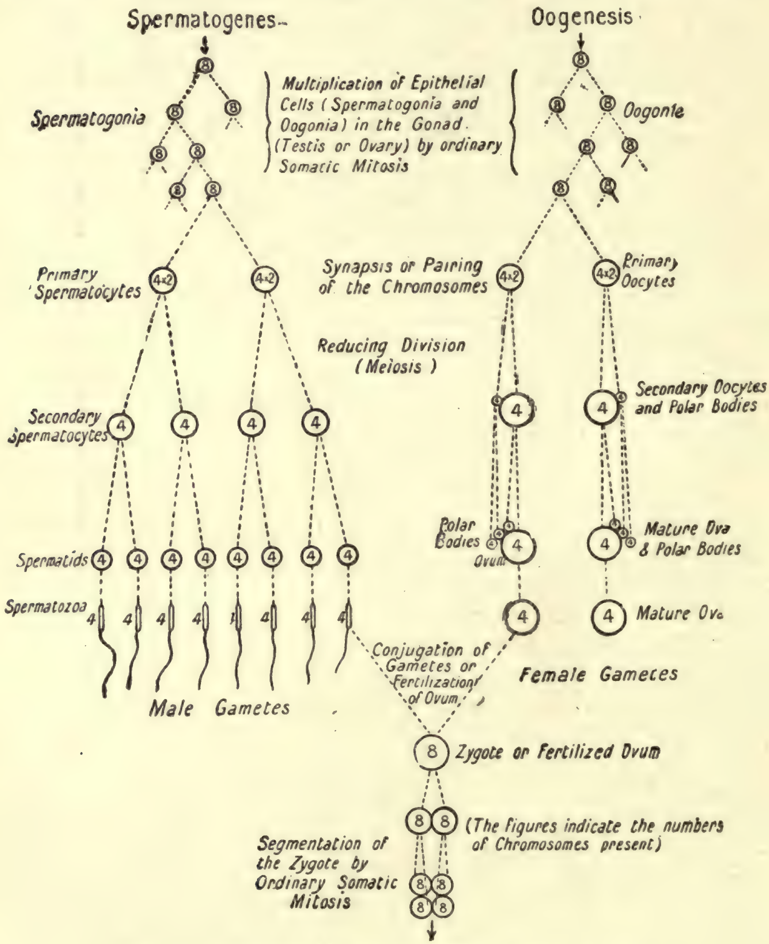


FIG. 126.—Diagram of gametogenesis.—From Dendy.

are double as the result of synapsis, and they segment into chromosomes. These chromosomes are bivalent, and so we have only the haploid number present. An amphiaster is formed, and the chromosomes become arranged upon the equatorial plate, but instead of this taking place in the middle of the cell, it is right

out near the periphery. A splitting of the chromosomes occurs, and the anaphase is entered upon. With the consequent division of the cytoplasm comes a marked difference from sperm formation. Instead of the cell dividing equally it splits into one large cell, and one very small one that contains little more than a haploid group of bivalent chromosomes. These two daughter cells may be termed the **secondary oöcytes,** but, on account of their striking difference both in size and fate, the large cell is spoken of as the **ovum,** and the small one as the **polar body.** In many animals no further changes are undergone while the egg remains in the ovary, and it is not until after it is shed that the next division occurs. This division is an ordinary and not a reducing one, and, as far as the distribution of the cytoplasm is concerned, is similar to the one preceding it. That is to say, the result is a large cell, now termed the mature ovum, and another, or second, **polar body.** The first polar body may also divide into two, and although it does not always do so, it may be considered that it should divide in typical and primitive cases. Thus from the primary oöcyte there are produced four cells which, however, are not equal in size and potentialities, as are the spermatids, but consist of one large mature ovum capable of development if fertilised, and three minute polar bodies which cannot develop and have, as it were, sacrificed their cytoplasm to produce one large ovum.

The relation between the two processes of germ cell formation, or, as they are collectively termed, the **maturation of the gametes** in the male and female, can be briefly set out in the following way :—

They are alike in—

(*a*) Their nuclei contain the haploid number of chromosomes the result of a meiotic and one subsequent division.

(*b*) Their chromosomes are alike in form, size and with few exceptions in number.

(*c*) Generally they can develop only after union.

They differ in—

Spermatozoon.	*Ovum.*
(*a*) Little cytoplasm.	Much cytoplasm.
(*b*) No food or yolk.	Always contains yolk and sometimes very large amount.
(*c*) Actively motile.	Non-motile.
(*d*) Centrosome present.	Centrosome absent.
(*e*) One of four similar cells derived from the spermatocyte all being functional.	One of four dissimilar cells derived from the oöcyte, the other three non-functional.
(*f*) Usually completely matured and formed in testis.	Usually formed in ovary, but not matured until after discharged.

The ova of different species vary in the amount and distribution of food material they contain, and also in the way in which they may be protected by the development of enclosing membranes. While in the ovary the egg is contained within a follicle which may fit closely round it, or may enlarge and become vesicular as in the Mammal, when the egg with a certain number of cells surrounding it lie to one side. While in the ovary two enclosing egg membranes may arise. Firstly, there is an envelope actually secreted by the ovum itself; this is termed the **primary egg membrane,** or **vitelline membrane,** and is usually very thin and structureless, but may be thicker and perforated by minute radial pores, when it is designated the **zona radiata.** In some cases it may even consist of an internal zona and an external clear membrane.

A **secondary** or **follicular membrane** may also be developed, but this is a product of the follicular cells, and not of the ovum itself. In many animals it is hard to distinguish how much of the envelope around the ovum in the ovary is primary and how much is secondary. Generally, in the Insects and Bony Fishes, the follicular membrane is quite distinct, and termed the "**chorion.**" Often these two membranes are perforated at one point by a tiny canal, the **micropyle,** which allows the sperms to reach the ovum.

When the ovum is ready it escapes from the ovary by the actual rupture of the follicle, a process that is termed **ovulation.** It makes its way to the oviducal funnel, and as it passes down the oviduct it may have deposited around it, as the result of the activity of the oviducal glands, one or more **tertiary egg membranes.** These may consist of a jelly-like mucilaginous substance as in *Rana*, or an albuminous layer as in *Scyllium* and the fowl, and in the case of these two animals, the dogfish has, in addition, a chitinous case, while the fowl has a calcareous shell. The provision of any or all of these membranes and their nature varies to meet the requirements of the conditions under which the egg is laid and develops.

Finally, the ovum itself may be provided with a large or small amount of food material, the **deutoplasm,** usually in the form of tiny granules, the **yolk spheres.** In certain animals, *e.g. Amphioxus* and the higher mammals, this supply is quite small and fairly evenly distributed throughout the cytoplasm of the ovum, and such an egg is termed **homolecithal.** On the other hand, and more commonly, there is a large amount of yolk present, and as it is unevenly distributed the ova are termed **heterolecithal.** In some forms, like Insects and Crustacea, it is concentrated towards the central part of the egg, leaving the peripheral protoplasm more or less free, a condition known as **centrolecithal.** The dogfish and the fowl have eggs with an enormous amount of yolk that is concentrated all at

one side or pole, and this condition is termed **telolecithal.** Indeed, such a large amount of yolk is present that it results in the active cytoplasm of the ovum being confined to a small area, the **germinal disc,** which contains the nucleus or **germinal vesicle,** as it is frequently termed, and is situated at one point of the surface. The question of the amount and distribution of the yolk is not an important matter from the point of view of the fundamental structure of the egg, since it is all non-active food material, and so a question of detail. On the other hand, it is of extreme importance to the changes occurring after fertilisation, since it determines to a large extent the way the early development can proceed.

With this general description of the germ cell we can leave the study of Cytology and pass on to consider what happens when the germ cells unite in certain species of Chordata.

CHAPTER XV

EMBRYOLOGY

Fertilisation, Segmentation and Germ Layer formation.

THE study of **Embryology,** or the development of animals, may well commence with the act that marks its inception, namely, **fertilisation,** by which is understood the fusion of the nucleus of a male gamete or spermatozoon with that of a female gamete or ovum, *i.e.* the constitution of a new individual. The ovum, as we have seen, is a large immobile cell often of great size, owing to its contained yolk. It always contains a nucleus, termed the **female pro-nucleus.** The sperm is little more than a **male pro-nucleus** with an accompanying centrosome and a tail, whereby it is able to move more freely. By some means or other, in those animals where fertilisation is internal by an act termed copulation, the spermatozoa are brought into proximity with the ovum. As a rule, numerous sperms surround one ovum, and by means of their perforating caps, aided by the active movements of the tail, start to bore their way into the egg, which sometimes puts out a small receptive process to meet one of them. Typically only one sperm penetrates the egg, whose membranes then appear to undergo a rapid physical or chemical change that prohibits the entry of further sperms. If several should enter the ovum, as sometimes happens in large eggs, only one of them is functionally active, and the others simply degenerate. When the head has successfully entered the ovum, the tail is shed, leaving only the head and neck, which are, therefore, to be regarded as the essential parts. Once inside, the head enlarges to form a typical nucleus with a chromatin network, and while so doing it rotates in such a manner that the centrosome formed from the granules in the neck, is pointed in the direction of the female pro-nucleus. An aster arises around the centrosome, and this, together with the male pro-nucleus, moves towards the egg nucleus. While this is proceeding the chromatin granules of both pro-nuclei organise to form a typical spireme, and one of two courses may be followed.

The more common way is for the centrosome and aster to divide and the two poles to move apart, forming a spindle between them.

The two nuclei lose their membranes, and the spiremes segment to form the chromosomes, which arrange themselves on the equatorial line of the spindle, sometimes even remaining in two distinct groups. Each of the pro-nuclei contains the haploid number of chromosomes, so that when the two come together in this manner the typical diploid, or somatic number, is restored in the combined groups. It will be seen then, that if there were no reduction in the course of the production of the gametes, each fertilisation would result in the doubling of the chromosome number, a proceeding that could not possibly go on. From this point on the division proceeds as in typical mitosis. That is to say, the metaphase, anaphase and telophase supervene, resulting in the formation of two cells. The single ovum has thus been fertilised and has divided into two by one continuous process, and this division is termed **cleavage** or **segmentation,** and the resulting cells, the first **cleavage cells** or **blastomeres.** It will be seen then, that there is no loss of chromosome identity in the above phenomena, and, particularly in those cases where the chromosome groups do not mix, it is clear that each daughter cell has its chromosome complement made up, half of maternal and half of paternal chromosomes. The next division, or second cleavage, takes place almost at once, and results in the formation of the first four cleavage cells or blastomeres. In these, too, it can sometimes be clearly seen that half the chromosomes are descended from each parental germ cell, an important point in considering the question of inheritance.

The other method of fertilisation, while less common, is in some respects more primitive and not so abbreviated. An amphiaster is formed as before, but slightly to one side, while the two nuclei lose their membranes, and their chromatin granules, or spiremes if they have been formed, mix up indistinguishably. This results in the formation of one chromatin reticulum or spireme, which may be termed the **cleavage** or **fertilisation nucleus.** The amphiaster, sometimes not formed until this time, now takes up a central position, and the spireme segments to form the diploid number of chromosomes, which become arranged to form an equatorial plate. Even in this type there is some evidence to show that the paternal and maternal chromatin retains its individuality, and the presumption is strong, that the cleavage cells receive an equal share from both male and female parent. After the formation of the amphiaster the blastomeres are formed as in ordinary division.

In both types of fertilisation it is clear that the fertilised ovum starts its career with a chromatin content derived in equal parts from both parents. If, as we have reason to believe, the chromosomes constitute the bearers of parental characters, then it

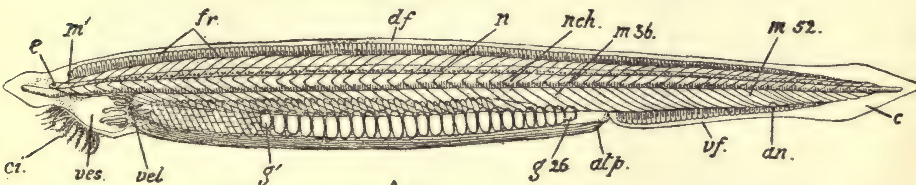
will be seen that, in spite of the difference in size between the two germ cells, the total inheritance of the new organism is derived equally from both male and female parent. This too has to be borne in mind when considering the phenomena of heredity. The sperm, in addition, introduced some stimulus, perhaps closely bound up with the centrosome, that is required to initiate development. It can be shown that this stimulus is nothing to do with the actual presence of the chromosomes themselves by experiments known as "artificial fertilisation." The eggs of some marine animals can be treated by the addition of certain soluble metallic salts to the sea-water in which they are contained, and in this way it has been found to be possible to supply the stimulus necessary to cause some eggs to segment. In certain cases, even, it has been found possible to produce advanced embryos in this way. But it is necessary to supply a stimulus, apparently a mechanical or chemical one, that is not ordinarily present in the environment of the egg in order to obtain this result, and under normal conditions this stimulus is introduced by the sperm.

As has been noted previously, certain animals ordinarily produce eggs that undergo development without fertilisation.. This is termed **parthogenesis,** and so the experiments just described are, on the whole, more accurately termed **artificial parthenogenesis.** When parthenogenesis occurs normally it is brought about by an entirely different means. It has been observed that during the production of the second polar body such eggs behave differently from those of other animals, and either the second polar body is not formed at all or, if it is, then, before its cytoplasm separates from the parent mass, its nucleus returns and reunites with that of the ovum. So that in these cases the second polar body, as it were, takes on the function of the sperm with the twofold result that the diploid number of chromosomes is restored and segmentation commences.

Amphioxus.

In order to get a clear idea of the main features of the embryology of the CHORDATA it is necessary that they should be considered briefly in several types, and we take first of all *Amphioxus lanceolatus,* where certain of them are presented in a simple condition. *Amphioxus* itself is a small somewhat fish-shaped form, growing to a length of about two inches. It is found at certain spots on the British coast, but more commonly in the Mediterranean, and allied species are found in the shallow seas of many parts of the world. It is almost transparent, and, although spending most of its time partly embedded in the sand, with only its mouth and anterior end protruding, it can swim and burrow into the sand very rapidly.

Compared with such an animal as *Scyllium*, for example, it is very simple in structure. It has no cranium nor sense organs, nor is its brain nearly so well developed. No cartilaginous skeleton is present, and even though it has a mouth, this is a circular orifice not provided with any structures that can be looked upon as jaws. No sign of paired fins is present, and all its systems are much less complicated with the one exception of the gill clefts, which are very numerous. The actual structure of the adult, however, does not concern us here, and it is sufficient to note that while it is undoubtedly highly specialised along certain lines, it is a representative of one of the most primitive groups of **Chordates** alive to-day, and so of considerable interest in comparative anatomy. Its embryological changes are also specialised, but, nevertheless, they illustrate certain funda-



A.

FIG. 127.—*Amphioxus*, general view.—From Bourne.

A, *an.*, anus ; *atp.*, atriopore ; *c.*, caudal fin ; *ci*, buccal cirrhi ; *df*, dorsal fin ; *e.*, eyespot ; *fr*, fin-rays ; g'., g^{26}., the twenty-six pairs of gonadial pouches ; m'., the first, m^{36}., the thirty-sixth, m^{52}., the fifty-second myotomes ; *n.*, neural tube ; *nch.*, notochord ; *vel.*, velum, in front of it are the finger-like processes of the wheel organ ; *ves.*, vestibule ; *v.f.*, ventral fin.

mental points in a very clear manner, and it is for that reason we treat of it here.

The fertilised ovum of *Amphioxus* is a minute spherical body about ·10 mm. in diameter. While the yolk that it contains is more abundant towards one pole, and so, strictly speaking, it is telolecithal ; yet there is so little present, and it is not entirely confined to one end, that it is often considered as homolecithal. Shortly after fertilisation the second polar body is extruded at what is termed the animal pole of the egg, and this is followed later by the first cleavage. The first division is **holoblastic,** that is to say, it passes completely through the ovum, and it takes place in a plane passing through the middle of the two poles. Shortly after, the second cleavage takes place, at right angles to the first, but still through the middle of the poles. Thus, after these two **meridional divisions,** the egg comes to consist of four equi-sized cells, each being half in the animal and half in the vegetative pole. The third division takes place at right angles to the other two, and is often termed **equatorial,** although, as a matter of fact, it is nearer one pole

than the other, and cuts off four smaller cells at the animal pole from four larger ones at the vegetative pole. The eight cells are

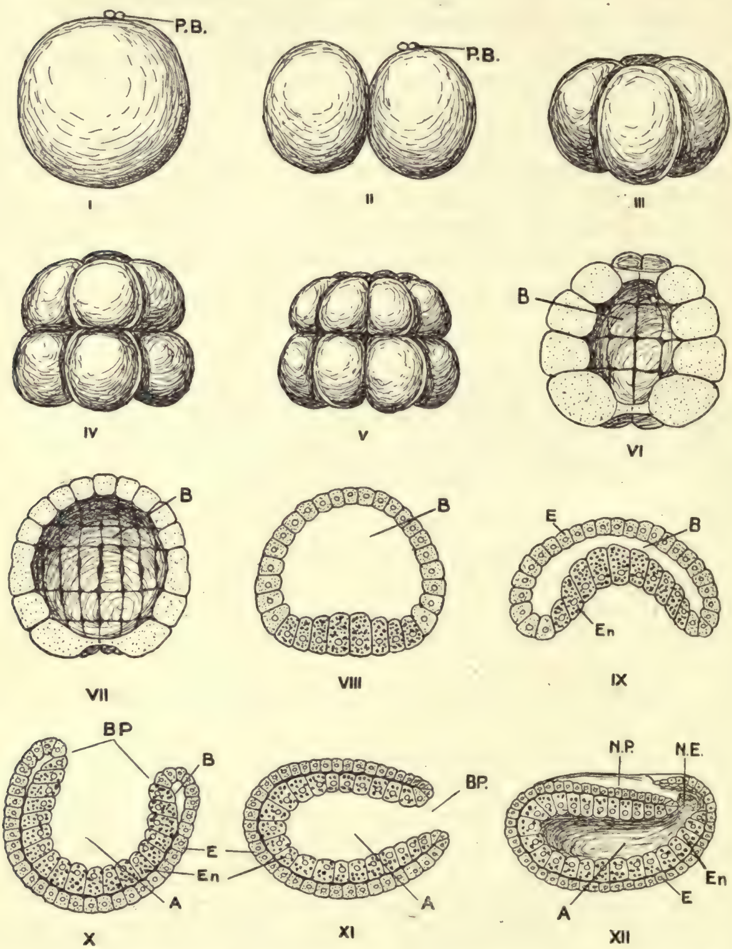


FIG. 128.—*Amphioxus*, early cleavage. I.–VII., and XII., adapted from Ziegler, after Hatchek. VII.–XI., adapted from Morgan.

I., ovum unsegmented; II.–VI., first five cleavages; VI. and VII., blastula stage; VIII., section of blastula just before gastrulation; IX. and X., sections of successive stages in gastrulation; XI., section of fully formed gastrula; XII., median view of half a late gastrula with neurenteric canal formed.

A., archenteron; B., blastocœl; B.P., blastopore; E., ectoderm; En., entoderm; N.E., neurenteric canal; N.P., neural plate; P.B., polar body.

turned into sixteen by the simultaneous formation of two meridional cleavages, and then into thirty-two by two latitudinal divisions.

Very frequently certain irregularities in division have appeared by this time, and after it segmentation is not so regular, the smaller cells at the animal end divide more rapidly than the larger yolk-laden ones at the other pole. While these divisions have been in progress a cavity has appeared in the centre of the cells, and so very soon we have produced a characteristic hollow sphere, the **blastula,** composed of a single layer of cells surrounding a central space, the **blastocœl** or **segmentation cavity.** This is a noteworthy stage, and recalls the condition in certain forms of colonial Protozoa, *e.g. Volvox.* The cells at the upper or animal pole are smaller and contain less yolk than those at the lower or vegetal pole.

The next step is an important one, since it consists in the transformation of this **embryo,** as a developing egg is termed, with but a single layer of cells into one with two layers. This process we term **gastrulation,** and it occurs in the following way. The lower pole becomes flattened, and then slowly this flattened area folds in and finally, with the obliteration of the segmentation cavity, lies next to the cells of the other pole. The result is a hollow cup-shaped embryo, the **gastrula,** composed of two layers of cells, an outer covering of small cells derived from the animal pole, and an inner lining of larger vegetative cells. In this way we have formed an internal cavity, the **primitive gut** or **archenteron,** which opens to the exterior by a wide circular aperture, the **blastopore.** The cells lining this cavity are termed the **entoderm** (or in older terminology hypoblast), and the external layer of cells the **ectoderm** (or epiblast). Thus the process of gastrulation, resulting in the laying down of the two **primary germ layers,** as they are termed, has led to the formation of a diploblastic embryo which, in the possession of these layers, of a single internal cavity and of a single external opening, recalls in its essentials the condition permanent in an adult Cœlenterate like *Hydra.* This likeness is made more obvious when the embryo lengthens and the blastopore becomes considerably reduced.

While this lengthening is in progress, a strip of ectodermal cells along the middle of the flatter dorsal surface becomes delimited from the surrounding cells and sinks slightly below the level of the remaining ectoderm. This constitutes the **neural** or **medullary plate,** and it extends from the upper lip of the blastopore forward almost to the anterior end. The cells bordering on this strip become slightly raised up to form the **neural folds** or **ridges,** and these gradually grow together so as to roof over the neural plate, save for a small circular area, the **neural pore,** at the front end. The process of enclosing the plate at the hinder end is also aided by the upward growth of the lower lip of the blastopore, so that this aperture becomes closed. While the general ectoderm has in this way been

growing over it, the neural plate has become curved downwards in the middle, thus leaving a small space under the superficial ectoderm. Owing to the way in which the lower lip of the blastopore grows upwards it closes the opening of the archenteron to the outside, but leaves a small aperture, the **neurenteric canal,** which puts the archenteric cavity in communication with the space above the neural plate. Eventually this plate becomes more and more folded until, finally, its two edges meet and fuse in the mid-dorsal line and so forms the **neural tube,** which is the forerunner of the central nervous system. It will be seen then that right from the very beginning the central nervous system is hollow, dorsal in position, and represents a specialised insinking of part of the original ectoderm,

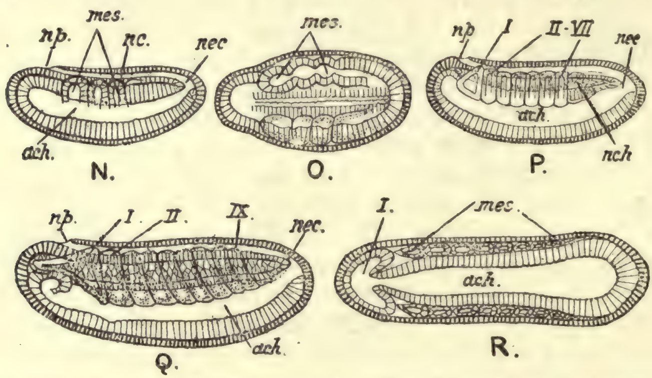


FIG. 129.—*Amphioxus*, later cleavage.—From Bourne, after Hatschek.

N., sagittal section of an embryo with three mesoblastic somites ; O., horizontal section of the same embryo ; P., sagittal section of an older embryo ; Q., sagittal section of an embryo with nine pairs of mesoblastic somites ; R., horizontal section of an embryo of the same age showing the origin of the head-cavities ; *ach.*, archenteron ; *mes.*, mesoblastic somites ; *n.c.*, neural canal ; *nec.*, neurenteric canal ; *np.*, neuropore ; I.–IX., the several pairs of mesoblastic somites ; *nch.*, notochord.

all important points. The neuropore and neurenteric canal remain open for some time, but finally both close.

While the formation of the neural tube has been taking place a series of changes have occurred in the archenteron. At an early stage it can be seen that the cells of the dorsal portion of the entoderm are smaller than those on the sides and floor of the cavity, and these dorsal cells become arranged in three longitudinal grooves, of which the median is first to appear. By the time the neural plate is roofed with ectoderm these grooves have become well marked, and in transverse section present the appearance of three pocket-like outbulgings from the archenteric cavity. The median of them is quite a narrow groove. During further growth its sides approximate and their cells interlock, and, finally, about the same time as

the neural tube is formed, it becomes cut off from the dorsal wall of the archenteron as a solid rod of cells. This is the **notochord** or **chorda dorsalis,** and although when first formed it does not extend to the anterior end of the body it does so later. Its cells undergo a considerable amount of modification, becoming highly vacuolated and producing the characteristic notochordal tissue. The notochord, then, arises from the mid-dorsal wall of the archenteron, and it is looked upon as a structure of such importance that the possession of a supporting rod of tissue derived in this way, and exhibiting its striking structural characteristics, is regarded as being one of the fundamental attributes of the Phylum CHORDATA, marking it off from all other Phyla.

While the neural tube and notochord have been forming, the front part of the lateral grooves has given rise to a series of hollow sacs, the mesodermal somites. These arise by the grooves closing off from the gut on each side in pairs of diverticula, one behind the other. This is the first indication of metameric segmentation, another fundamental characteristic of the Chordates. These outgrowths, as we have seen, are hollow from the beginning, and their cavities represent the cœlom, which since it has been derived directly from the gut in this particular type, is termed an **enterocœl.** A number of such pairs of somites are formed, but with their more rapid development we find that the posterior ones arise as solid blocks of cells in which the cavity is formed later. The first of the pouches to arise in the manner just described is really the third pair of somites, there being two other pairs situated more anteriorly. The first two pairs of somites arise in a somewhat similar manner, but as four independent sacs growing out from the anterior end of the dorsal archenteric wall in front of and not connected with the lateral grooves. When the enterocœlic pouches and the notochord have been cut off from the archenteron, the cavity left surrounded by entoderm can be spoken of as the **definitive gut,** the **enteron** or **mesenteron.**

Turning now to the enterocœlic pouches we see from the manner of their formation that they come to constitute a group of cells interposed between the ectoderm and entoderm, and so they are termed the middle layer or **mesoderm** (or **mesoblast**). At the front end the mesodermal somites of the two sides are opposite, but further back they come to be alternate. The pouches, as soon as they are formed, begin to enlarge by extending in a ventral direction between the entoderm and ectoderm, and their walls differentiate into three regions. The outer portion adjoining the ectoderm becomes thin and is known as the **parietal** or **somatic mesoderm.** The cells surrounding the gut wall likewise thin out to form the

visceral or **splanchnic mesoderm.** The cells of the remaining part, namely, that bordering on the notochord and neural canal, enlarge in the horizontal plane to form a comparatively thick plate to which the term **myotome** is applied. It is sometimes convenient to differentiate between the myotome and the other two portions, *i.e.* the splanchnic and somatic mesoderm, and so for these we use the inclusive term **lateral plate.** The enlargement of the myotome reduces the cœlomic cavity in its vicinity to a small cleft, the

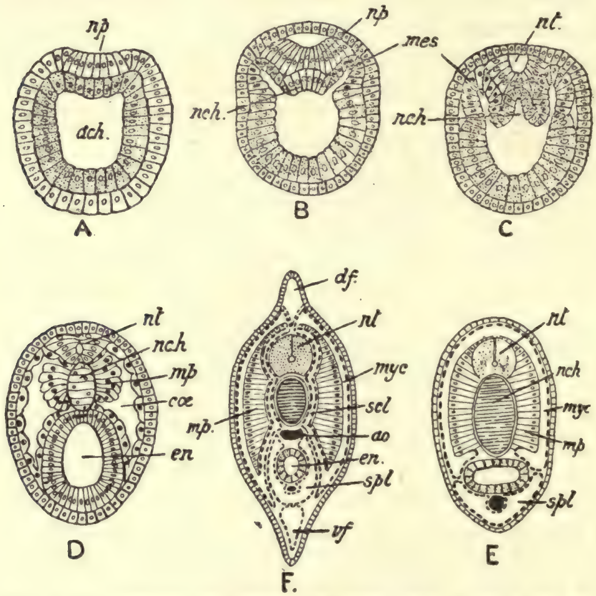


FIG. 130.—*Amphioxus*, transverse sections.—From Bourne, after Hatschek.

A, B, C, transverse sections of embryos of *Amphioxus* of different ages, illustrating the formation of the neural tube, notochord, and mesoblastic somites. *ach.*, archenteron; *mes.*, mesoblastic somites; *nch.*, notochord; *np.*, neural plate; *nt.*, neural tube. D, transverse section through an older embryo in which the mesoblastic somites are completely separated from the archenteron. *mp.*, muscle plate; *cœ.*, cœlom; *en.*, mesenteron; the other lettering as above. E, diagrammatic transverse section through a larva with five gill-slits. *myc.*, myocœle; *spl.*, splanchnocœle. F, diagrammatic transverse section of a young *Amphioxus* shortly after the metamorphosis; the section is taken between the atriopore and anus. *ao.*, aorta; *df.*, dorsal fin; *scl.*, sclerotome; *vf.*, ventral fin; the other lettering as above.

myocœl. On the other hand the remaining part of the cœlom, now known as the **splanchnocœl,** enlarges, and, finally, the partitions between the successive splanchnocœls break down, giving rise to the one large cœlom of the adult. While the union of the ventrally situated portions of the enterocœlic cavities is taking place, a series of partitions arise that shut off the myocœls which do not run together.

We have thus reached a stage of considerable importance in which the three primary germ layers have been established: an ectoderm on the outside, which also gave rise to the neural tube; an entoderm on the inside destined to produce the whole of the gut, including the pharynx and a mesoderm, which from its commencement included a hollow, the cœlom, and is differentiated into myotome, somatic and splanchnic portions. The further history of the embryo of *Amphioxus*, while interesting, is fairly highly specialised, and relates to the formation of the various structures characteristic of the adult in particular, and not so much to Chordates in general. The development so far may be considered as that of a primitive Chordate, whose egg contains but little yolk, and whose early stages are not complicated by the special requirements of the young embryo, and we may now pass on to see how a similar stage is reached in other forms.

Rana.

The eggs of the frog when laid are spherical bodies about 2–3 mm. in diameter and surrounded by a thin coat of albuminous matter composed of the tertiary egg membranes. As it floats in the water it will be seen to consist of an upper or animal hemisphere, dense black in colour owing to the presence of pigment in it, and a lower or vegetative hemisphere, somewhat larger and white or greyish white in colour. The egg is provided with a plentiful supply of yolk and is **telolecithal,** that is to say, the yolk is concentrated towards the vegetative pole. At the time the egg is laid its nucleus, situated towards the top of the animal pole, is arrested in mitosis preparatory to giving off the second polar body and so becoming mature. The sperms are shed in the water where fertilisation occurs and the entrance of the spermatozoon apparently supplies the stimulus leading to the extrusion of the second polar body. After the egg has been in water a short time the albuminous envelopes, of which three can be recognised, absorb water and swell up until they reach the size of a small pea. During the processes of formation, and particularly during the fertilisation and maturation of the egg, its contents are so organised that the ovum as a whole is not merely divided into poles, but has a definite bilateral symmetry which determines the direction of subsequent divisions.

The first cleavage is holoblastic, completely dividing the ovum into two cells, and it is finished about two and a half hours after fertilisation. The segmentation is indicated externally by the appearance of a furrow starting in the animal pole and then running completely around the egg, but the two cells remain close together,

each being hemispherical and do not separate as much as in *Amphioxus.* The second cleavage, also holoblastic, takes place in a plane passing through the centres of the animal and vegetal poles in a plane at right angles to the first and results in the formation of four blastomeres. The third division, as in *Amphioxus,* is in a plane at right angles to the other two, but although complete, is well above the equator and cuts off four smaller cells at the animal pole from

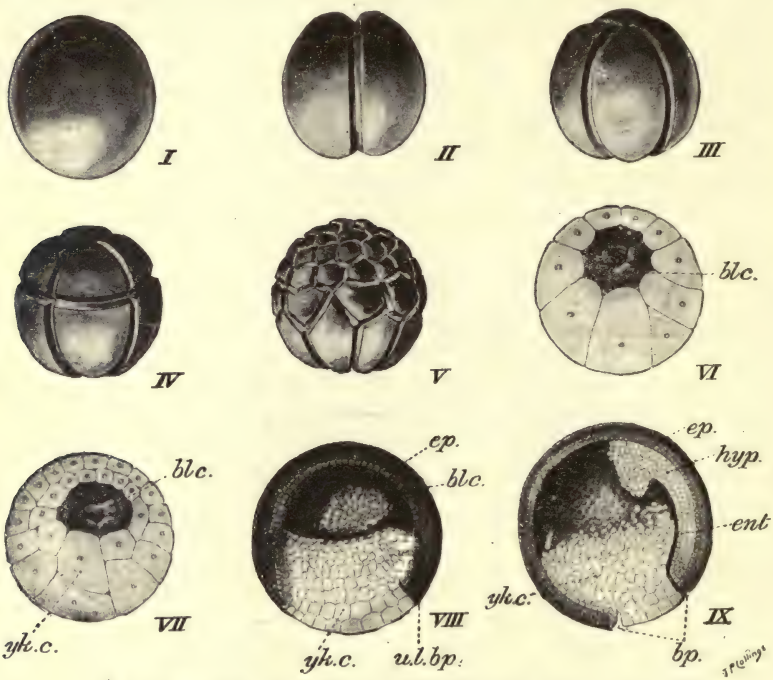


FIG. 131.—*Rana,* early stages segmentation.—From Dendy.

I., the fertilized ovum ; *II.–V.*, segmentation of the ovum ; *VI.*, blastula ; *VII.*, modified blastula, with wall composed of more than one layer of cells ; *VIII.*, commencement of gastrulation ; *IX.*, the modified gastrula stage (*VI.–IX.* in vertical section). ***blc.***, blastocœl or segmentation cavity ; ***bp.***, blastopore ; ***ent.***, enteron ; ***ep.***, epiblast ; ***hyp.***, hypoblast ; ***u.l.bp.***, upper lip of blastopore ; ***yk.c.***, yolk-containing cells.

four much larger ones at the vegetative pole. The fourth cleavage is initiated by the appearance of a pair of furrows bisecting the apical angles of the cells of the animal pole and it extends more slowly down over the four vegetal cells, but finally produces sixteen cells. Somewhere about this stage the segmentation proceeds less regularly and takes place more rapidly at the animal pole, as if it were hindered at the vegetative pole by the presence of too much

inert yolk material. The result is that the number of small dark cells is greater than that of the light-coloured cells.

When the eight-celled stage is reached, each cell rounds off internally so as to leave a small internal space, the beginning of the blastocœl or segmentation cavity, which right from its commencement is eccentric in position lying nearer the animal pole. This increases in size and is quite well marked when there are from 32–64 cells present, and so the embryo as a whole is now a **blastula** whose wall is much thinner at the animal pole than elsewhere. Even by the time the sixty-four-celled stage has been reached, we find a departure from the procedure found in *Amphioxus*, for some of the cells have divided in a plane tangential to the surface in such a manner that one of the daughter cells comes to lie on the inside. Thus it is that all divisions are not marked on the outside and the wall of the blastula, instead of consisting of a single layer of cells, comes to consist of several layers. The fully formed blastula is spherical and slightly larger than the ovum and the symmetry indicated in the egg has become more obvious. The anterior wall of the segmentation cavity is a little thicker than the hinder while the pigmented cells extend a little further down on the posterior side. Also the small cells at the animal pole have become differentiated into an outer compact **superficial** or **epidermal layer** and an underlying more irregular and looser "**nervous layer.**" The external area of pigmentation has also spread out so that it covers more of the outside of the blastula than it did of the ovum.

The process of forming a double layered embryo or gastrula is very different from that in *Amphioxus*. The first indication of the change is the appearance of a slight irregular horizontal groove on the posterior side of the blastula. This soon assumes a crescentic shape and becomes more strongly marked as the cells on its upper or convex border are deeply pigmented while those on the lower edge are white. A section through the embryo at this stage reveals the meaning of the crescent. It is due to a double process; in the first place the cells of the animal pole are actually growing downwards at the point to enclose the vegetative cells and these in their turn are arching up into the animal hemisphere. The edge of the crescent extends sideways further and further over the vegetative cells until finally its edges meet and it forms a slightly oval area. This is the blastopore, and owing to its position with regard to the orientation of the embryo as a whole, we are able to see now that the original point at which it started was the dorsal lip, and so the ventral lip is the last to be formed. The blastopore when first completed lies on the equator at the posterior end, but as development proceeds it becomes smaller and smaller, and the centre of gravity of the embryo

shifts slightly, bringing about a rotation, so that the blastopore comes to lie well above the equator. It is visible for some time and is filled with a small group of the white vegetative cells, which is termed the **yolk plug.** While these external changes have been taking place no less important ones have occurred internally. The

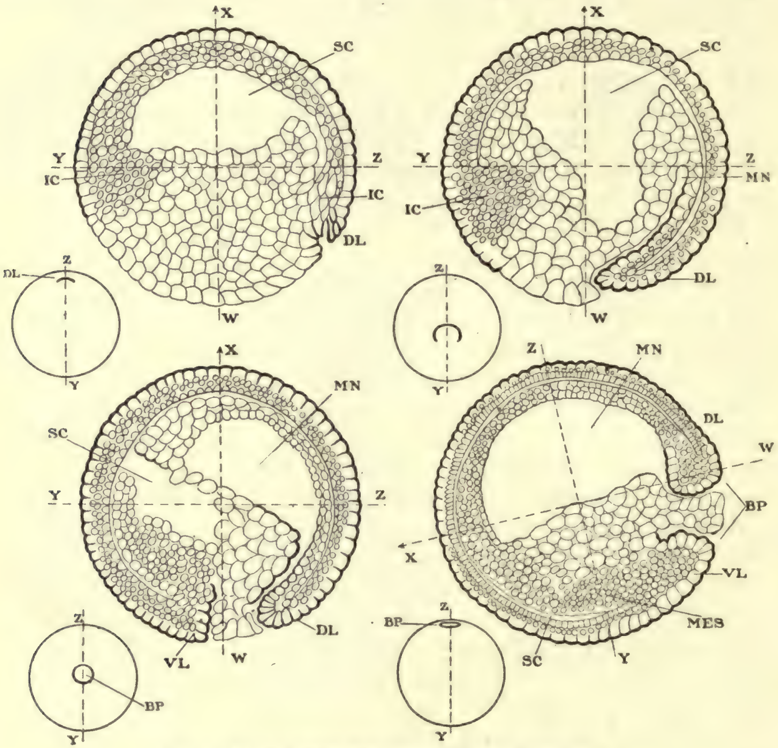


FIG. 132.—*Rana,* sections.—From Marshall.

The four small figures represent the segmenting egg, seen from its lower pole, and illustrate the formation and shifting of the blastopore (BP.). The four large figures are sections of the egg taken vertically through its horizontal axis Y.Z., and represent four stages in the formation of the mesenteron. Notice the rotation of the egg through more than 90°.

D.L., dorsal lip of blastopore ; I.C., intermediate cells ; MN., mesenteron ; SC., segmentation cavity or blastocœl ; V.L., ventral lip of blastopore ; WX., axis of embryo, which is at first vertical and subsequently antero-posterior ; YZ., axis of embryo, which is at first horizontal and subsequently vertical or nearly so.

vegetative cells push their way up as a moderately thick layer underneath the dorsal lip of the blastopore which becomes turned in and moves slightly with them. They move round the dorsal side of the segmentation cavity, leaving a small irregular cleft between themselves and the ectoderm cells growing over them, and finally they reach the yolk cells of the opposite or anterior end.

This process is completed about the time that the outline of the blastopore is completed, and thus we have produced a two-layered embryo. The outside pigmented layer is the **ectoderm** and the inside cells constitute the **entoderm** while between them is the cleft representing the **blastocœl** which gradually becomes obliterated as in *Amphioxus*. On the dorsal side the entoderm cells are in a layer two or three cells deep, while on the ventral side they are much larger, more irregular and many cells deep. A group of these larger cells forming the yolk plug practically fills the blastopore. These ventral cells are heavily laden with yolk and constitute a food store upon which the embryo relies for some time to come. The space within the entoderm cells is, of course, the **archenteron**, and it may communicate with the exterior by a small cleft under the dorsal lip of the blastopore. Thus we see that while the details of the process differ considerably in *Amphioxus* and *Rana*, the result of gastrulation in both cases, with certain modifications in the frog that will be considered immediately, is to produce an embryo with an ectoderm, an entoderm, an archenteron and a blastopore: a typical diploblastic condition and the differences are in the main due to the amount of yolk present in the frog's egg

While we have not yet taken notice of the mesoderm, as a matter of fact it has been formed for some considerable time, and the above description of the gastrula is not strictly speaking accurate, for when the stage just dealt with is reached a good deal of mesoderm is already present. The simple diploblastic condition in *Rana* is more theoretical or potential than actual, and the precocious appearance of the mesoderm prevents its realisation in anything like a complete form.

If we examine closely a section through the embryo when gastrulation is commencing we shall find at the dorsal lip of the blastopore, where the ectoderm and entoderm cells are in contact, another small group of cells that are destined to form the mesoderm. They are right in the bend of the lip between the ecto- and entoderm, with both of which layers they are continuous. As the blastopore lip extends laterally, these cells spread with it, so that when the margins join up the primitive mesoderm cells also unite and thus come to constitute a mesoderm ring within the lip of the blastopore. The dorsal lip commences fairly high up, and as it extends, it first moves down ventrally and during this period it leaves behind it a band of mesoderm, so that the ring is much deeper on the dorsal side than on the ventral. Furthermore, the dorsal extension of the entoderm carries the mesoderm with it so that it soon becomes fairly extensive. At first more or less closely connected with the entoderm, the mesoderm cells are gradually delimited fairly sharply

from it, giving rise to a more definite layer that first appears in the dorso-lateral regions. The presence of the yolk-laden cells in the ventral half of the embryo delays matters somewhat, but cells are given off by the dorsal mesoderm which pass further and further ventrally and form a more or less continuous layer of mesoderm that separates the yolk-laden entoderm from the ectoderm. In the actual mid-dorsal line, particularly near and in front of the blastopore, the mesodermal cells are slightly differently related to the other layers and the formation of the notochord leads to certain modifications.

Along the axial line the rudiments of the notochord, the mesoderm, the dorsal entoderm, and to a certain extent also the ectoderm, are not clearly separable and form an axial mass, while laterally to that the mesoderm is separated from both ento- and ectoderm. As the blastopore closes the slit between ecto- and mesoderm on each side passes inwards towards the middle line, but before reaching it turns downwards and stops. This leaves a thickened layer of ectoderm (the neural plate, *vide infra*), superficially and beneath it a sort of wedge-shaped vertical mass of cells, the notochord rudiment now cut off from the lateral mesoderm. The cleft separating ento- and mesoderm also passes inwards, but stops short of the middle line below and slightly lateral to the other slit, thus leaving the entoderm cells continuous right in the middle line with the notochordal cells and just lateral to this continuous with the lower portion of the lateral mesoderm mass, by this time fairly thick. Along the regions where the dorsal entoderm is continuous with the mesoderm in this way, shallow but nevertheless distinct grooves appear which are taken to represent enterocœlic invaginations homologous with those in *Amphioxus*. At a later stage the appearance of a slit cuts the notochord off from the entoderm leaving only a single layer of its cells to roof the enteron, and a

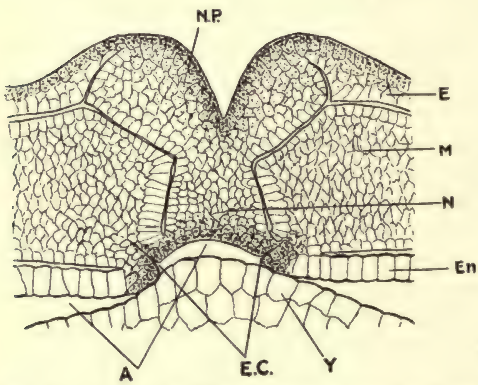


FIG. 133.—*Rana fusca*, transverse section through young embryo.—After O. Hertwig.

A., archenteron ; E., ectoderm ; E.C., traces of enterocœls ; En., entoderm ; M., mesoderm ; N., notochord ; N.P., neural plate ; Y., yolk cells.

similar cleft cuts it off from the ectoderm. In this way the notochord is formed.

We must now go back again to the stage when the blastopore is just completed, to consider the formation of another important structure. Here we find that the "nervous" layer of the ectoderm has thickened to form a moderately wide **medullary plate** which extends forwards from the dorsal lip of the blastopore to the front end. As the blastopore closes and the yolk plug is withdrawn, the lateral margins of this plate are elevated slightly to form the **lateral neural folds** which run from the sides of the blastopore to the anterior end, becoming more marked as they do so. At the front they turn inwards and unite in the middle line, so forming a **transverse neural fold** marking the front limitation of the medullary plate. The area contained within the folds, termed the neural plate, is somewhat thinner than the margins and a groove appears along its middle line, the **neural groove.** When this has been laid down a cleft appears beneath the plate and cuts it off completely from the underlying notochord as noted above.

Although the embryo is now in a triploblastic condition there is as yet no cœlom, and it will be as well to follow the developmental processes a little further so as to reach approximately the same stage in which we left *Amphioxus.*

The formation of the central nervous system is indicated, as we have seen, by the formation of the medullary plate, neural folds and neural groove. As development proceeds the groove becomes deeper and narrower and the neural folds pass towards the middle line. Finally they bend over and meet, but not simultaneously along their whole extent. They first come into contact at a place that will form the myelencephalon, so that from here onwards the differentiation into brain and spinal cord regions can be recognised. From this first point the fusion extends in both directions, but more rapidly towards the posterior end. As the union of the folds passes slowly forwards the transverse folds also meet, their fusion extending backwards until it reaches the fusion of the lateral folds at a point between the future fore and mid brain. This is, therefore, the last region to fuse and so can be considered as the neuropore, but it has only a transitory existence and soon closes. From the manner in which the lateral neural folds come together, the actual union takes place along the edges of the neural plate, so that only this structure takes part in the formation of the neural canal. The neural folds themselves are left outside the canal, between it and the covering ectoderm. Later they become broken up into groups of cells lying along the dorso-lateral region of the central nervous system, thus constituting the **neural crests** which are concerned with the development

of the nerves. As the blastopore closes it becomes slit-like and then fuses in the middle region, leaving an opening at each end. The neural plate extends right back to the dorsal lip of the blastopore and as it bends over and fuses to form the neural tube, it gradually closes over the posterior end of the upper aperture, but internally leaves at this point an open communication, the **neurenteric canal,** leading from the neural canal to the enteron as in *Amphioxus.*

Where the lips of the blastopore with their various approximated

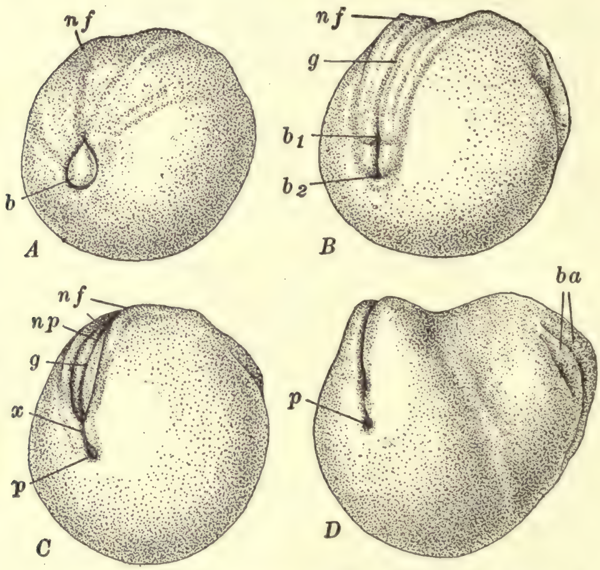


FIG. 134.—*Rana*, young embryos.—From Kellicott, after F. Ziegler.

A, blastopore nearly closed ; neural folds just indicated. B, blastopore becoming divided into neurenteric and proctodæal portions ; neural folds becoming elevated. C, neurenteric canal forming ; neural folds closing together. D, neural folds in contact throughout.

b., blastopore, containing yolk plug ; *b1*, rudiment of neurenteric canal (dorsal part of blastopore) ; *b2*, rudiment of proctodæal pit (ventral part of blastopore) ; *ba*, branchial arches ; *g.*, neural groove ; *nf*, neural folds ; *np*, neural plate ; *p.*, proctodæal pit ; *x.*, neural folds roofing the blastopore and establishing the neurenteric canal.

layers fuse, the cells of the ecto-, ento- and mesoderm are brought together into one undifferentiated mass known as the **primitive streak** down the middle of which runs a groove, the **primitive groove** marking the point of junction. The lower opening fuses internally, and so leaves an external pit lined with ectoderm. This is the **proctodœum,** and internally an evagination of the entoderm, the future rectum, grows out towards it.

Practically while the neural folds are closing the brain region

becomes differentiated into three enlargements, the **fore, mid** and **hind brain vesicles** clearly visible in longitudinal section at a slightly later stage. Very shortly after, a striking flexure occurs in the mid brain and as a result the fore brain is bent down at right angles to the rest of the central nervous system. The notochord extends from the posterior end forward to the end of the mid brain where it stops. Right in front of the fore brain a median tongue of cells, the **hypophyseal ingrowth,** passes inwards from the ectoderm and at a later stage a terminal group of cells leaves this and passes inwards to take up its position in front of the end of the notochord, under the floor of the hinder part of the fore brain. This group of cells is the rudiment of the hypophysis ; indications of the olfactory organs and ears as ectodermal thickenings by this time.

When the neural tube has been completed and the flexure of the brain has taken place, the embryo has elongated noticeably in the antero-posterior direction. Certain changes have also occurred in the enteron during this period of growth. With the separation of the notochord and mesoderm the whole of the dorsal region and the anterior end of the ventral portion is lined by a single layer of cells. A large number of yolk-laden cells still remain, forming a yolk mass in the posterior half of the ventral region of the enteric cavity. Their presence enables three regions of the enteron to be clearly differentiated. In front of them the enteric cavity expands to form the **fore gut,** a wide deep cavity lined by a single layered epithelium. This region will give rise first to the pharynx, and later to the œsophagus and stomach and at its antero-ventral end in the middle line is a short **oral evagination** that will later be met by an ectodermal invagination, the **stomodœum,** which is to form the mouth and buccal cavity. The hinder end of the enteron is characterised by being in communication with the cavity of the central nervous system, via the neurenteric canal, and also by an evagination that will later produce the rectum. This region, also lined by a single layer of cells, is designated the **hind gut.** Between them the dorsal wall is single layered, but the ventral wall many layered, owing to the presence of the yolk cells which also reduce the enteron to a narrow dorsal cleft. To this region the name of **mid gut** is given, and it will later give rise to the intestine of the adult.

Finally, we have to consider certain changes in the mesoderm. It has already been noted that the mesoderm extends laterally from the sides of the notochord and neural tube as a solid sheet of cells, separating the ecto- and entoderm, save that at the primitive streak region it is confluent with the other layers. With the development and flexure of the brain the mesoderm cells extend up into this head region. Here, however, they do not form a definite compact sheet,

but are represented by a number of scattered somewhat stellate

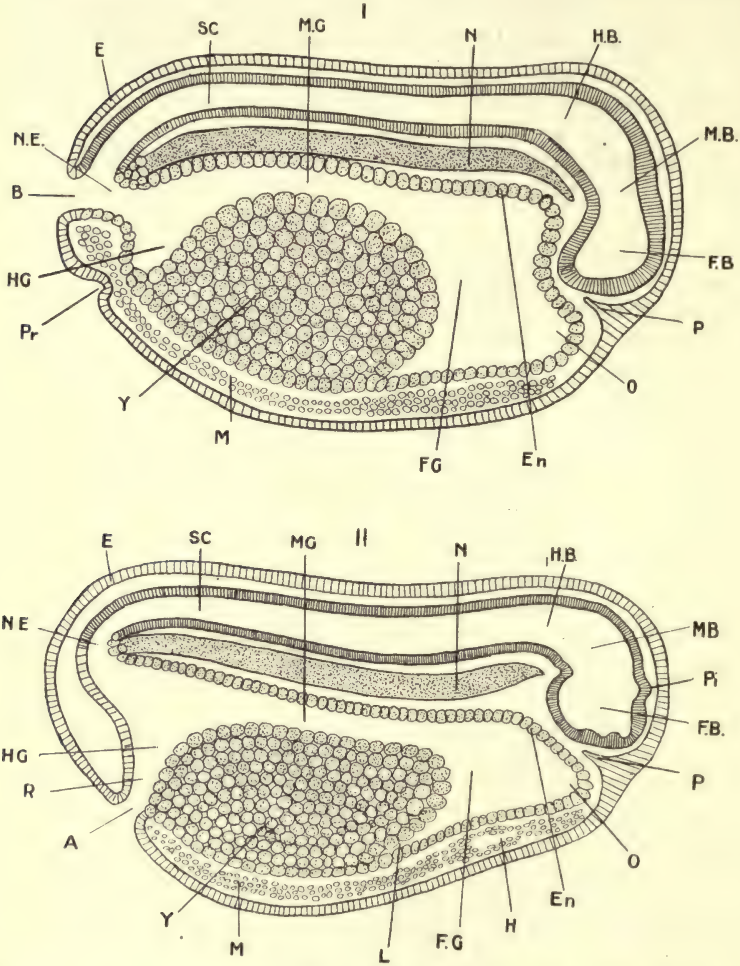


FIG. 135.—*Rana temporaria.* Diagrammatic sections of sagittal sections of young embryos: I., before closure of blastopore; II., after closure of blastopore.

A., anus; B., blastopore; E., ectoderm; En., entoderm; F.B., fore brain; F.G., fore gut; H., heart rudiment; H.B., hind brain; H.G., hind gut: L., beginning of liver diverticulum; M., mesoderm; M.B., mid brain; M.G., mid gut; N., notochord; N.E., neurenteric canal; O., oral evagination; P., pituitary ingrowth; Pi., pineal outgrowth; Pr., proctodœum; R., rectum; S.C., spinal cord; Y., yolk cells.

cells filling in the interstices between the brain and ectoderm and front end of the enteron. Mesoderm in this condition is frequently

referred to as **mesenchyme.** During the period dealt with above, the mesoderm in the middle region of the embryo along the side of the notochord becomes more solid and thicker, and constitutes the **segmental plate** or **myotomal region.** It is fairly sharply marked off from the thinner lateral portion which is the **lateral plate.** A cleft soon appears in this, thus forming the beginning of the cœlom, or more strictly the splanchnocœl, and this divides the mesoderm

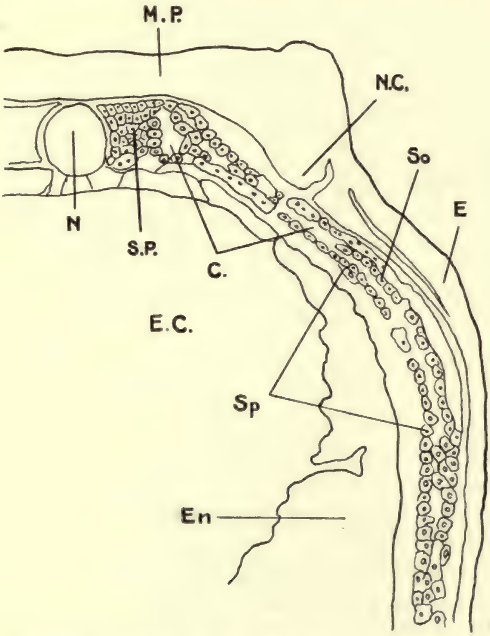


FIG. 136.—*Rana sylvatica.* Part of a section through the anterior part of the body of a young embryo; ectoderm and entoderm represented in outline only.—After Field.

C., cœlom; E., ectoderm; E.C., enteric cavity; En., entoderm; M., mesoderm; M.P., medullary plate; N., notochord; N.C., neural crest rudiment; So., somatic mesoderm; Sp., splanchnic mesoderm; S.P., segmental plate.

into somatic and visceral layers. A cœlom originating in this way as a split in a mesodermal sheet is often referred to as a **schizocœl** as opposed to an enterocœl as in *Amphioxus.* At first this cleft is confined to the upper part of the lateral plate, and it does not extend ventrally until considerably later, although it passes up into the segmental plate giving rise to rudimentary **myocœls.** This stage is reached as the neural folds begin to approximate, and as they do so the longitudinal bands of mesoderm begin to get cut up into pairs of

segments or **somites.** At the time of closure of the neural tube, three or four pairs of somites have been formed; the first of them lies at the end of the fore gut, and thence the process of somite formation passes posteriorly. It is noteworthy that such segmentation does not extend forward to the head region or laterally to the lateral plates. Here, then, we have the embryo in approximately the same stage of development as was reached in *Amphioxus*

Gallus, the Fowl.

In the fowl's egg we have an example of the extreme telocithal condition, for there is a very large amount of yolk all massed at one pole. This is a matter of considerable interest from the comparative point of view, since it leads to certain modifications in the process of development resulting, among other things, in the production of certain membranes. The mammal, whose egg is small and almost yolkless, has been derived from an ancestral form with a heavily yolked egg, and consequently we find certain peculiarities in its development paralleled in the fowl's egg, and the membranes are put to quite other uses, as we shall see. Fertilisation is internal and effected at the top of the oviduct, and segmentation commences straight away, so that by the time it is laid the process is well under way.

At ovulation the egg consists only of the so-called yolk which passes to the oviduct (in the fowl only the left ovary and oviduct are functional), where it has added to it the tertiary egg membranes. The ovum leaving the ovary is surrounded by a thin vitelline membrane, and in spite of its large size is only a single cell whose nucleus and active cytoplasm is confined to a small whitish area about 3 mm. in diameter on one side of it. The **germinal disc,** as this spot is called, is situated upon and continuous with the yolk, and the latter is composed of two different varieties of material, one white and the other yellow. A layer of the white yolk underlies the germinal disc and a neck of it extends downwards into the centre of the yolk, where it swells out to form a flask-shaped mass, the **latebra.** Around this the yolk is arranged in concentric layers of alternate thick layers of yellow and thin layers of white. The cytoplasm around the disc where it joins the white yolk is slightly darker in colour and forms a ring known as the **periblast.** When the egg is laid we find that there has been added to the ovum a thin layer of very dense albumen, the **chalaziferous layer,** which is continued out at each side into a tough twisted cord, the **chalaza,** whose function it is to keep the germinal disc uppermost, however much the egg may be turned about. Outside this is a thick layer of

less tough, but still fairly dense, albumen, and this in turn is surrounded by a thickish layer of more fluid albumen. These three albuminous layers constitute the so-called white of the egg. The albumen is confined in a tough bag, the shell membrane composed of a double layer of fibrous matter, and the two layers separate at the blunt end of the egg to include between them a small air chamber. Finally, overlying the shell membrane is the calcareous shell itself,

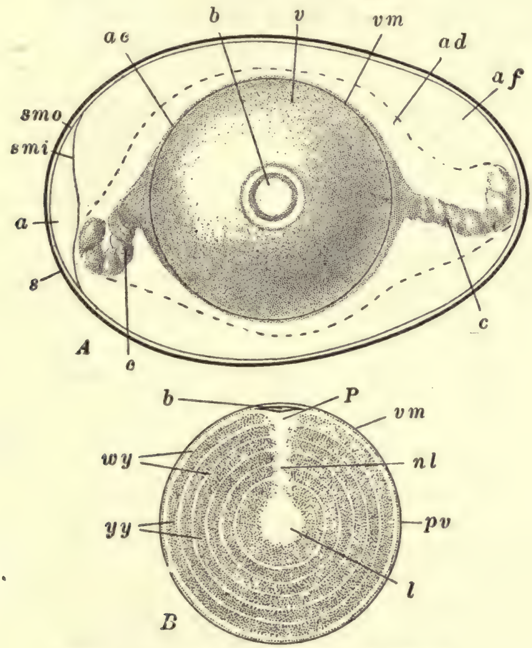


FIG. 137.—Hen's egg.—From Kellicott.

A, entire "egg," modified from Marshall. B, vertical section through the vitellus or ovum proper, showing the concentric layers of white and yellow yolk. *a.*, air chamber; *ac*, chalaziferous layer of albumen; *ad*, dense layer of albumen; *af*, fluid layer of albumen; *b.*, blastoderm; *c.*, chalaza; *l.*, latebra; *nl*, neck of latebra; P., nucleus of Pander; *pv*, perivitelline space; *smi*, inner layer of shell membrane; *smo*, outer layer of shell membrane; *v.*, vitellus or "yolk"; *vm*, vitelline membrane; *wy*, layers of white yolk; *yy*, layers of yellow yolk.

which when dry is porous and allows of the passage of gases and water vapour. All these structures are of the nature of tertiary egg membranes.

Maturation in the fowl's egg does not take place until just after it has entered the oviduct and been fertilised. With the entrance of the sperm the first polar body is extruded and immediately after that the second is given off. Polyspermy appears to be the rule, but although a number of spermatozoa enter the egg, only one takes

part in the act of nuclear fusion, the others after a while degenerating. The presence of such an enormous amount of yolk renders it impossible for the tiny mass of cytoplasm to control the whole ovum, and as a result we find that the cleavages are confined to one pole of the egg. Such a type of segmentation is termed **meroblastic** or **incomplete,** in opposition to the holoblastic or complete type.

The first cleavage is indicated about three hours after ovulation by the formation of a furrow in the middle of the germinal disc which extends over about half its diameter. Not merely does this groove fail to stretch across the disc, but it also does not reach the bottom of the cytoplasm. The second cleavage occurs in a plane at right angles to the first, so marking off four areas, the **blastomeres.** Typically the third cleavage is represented by a double furrow parallel with the first, so that the centre of the disc is divided into two rows, each containing four cells. Hereafter the cleavages become irregular, although it is sometimes possible to make out a fourth fairly regular cleavage in the form of a pair of furrows parallel with the second, so cutting the four cells on each side into central and peripheral daughter cells. While the third and fourth cleavages are making their appearance a horizontal cleavage takes place in the region of the central cells cutting off from under them a central unsegmented mass of cytoplasm. So that there is now a group of **central cells** completely circumscribed and surrounding it the **marginal cells** joining the periblast. The whole area of cells so formed is termed the **blastodisc** or **blastoderm.** The horizontal cleavage just noted widens until it forms a slit which is the **segmentation cavity** or **blastocœl,** or as it is often termed in this form the **subgerminal cavity.** Above this lie the central cells and below it the unsegmented cytoplasm now designated the **central periblast** to distinguish it from the original or **marginal periblast.**

Subsequent cleavages take place somewhat rapidly, until a large number of cells are produced, most of which are central cells, while the marginal cells are reduced to a small band around the periphery. Other cleavages have also occurred in the horizontal plane, so that the roof of the blastocœl is several cells thick. The nuclei of the marginal cells divide without accompanying cytoplasmic divisions and the daughter nuclei so produced wander out into the peripheral and finally into the central periblast. So that the periblast becomes transformed into a **syncytium,** that is, a continuous mass of protoplasm containing a number of nuclei without the corresponding cell divisions. Hundreds of tiny cells are formed by this time and the blastoderm begins to increase in size, partly from the growth and extension of its own cells, and partly by the addition of cells cut off from the periblast. The inner part of the periblast, which

gradually becomes cellular, is of considerable importance later, and is known as the **formative ring** or **germ wall.** During the process just described the central cells have become thinner and somewhat transparent so forming an internal area known as the **area pellucida,** while the marginal cells, composed in part of cells derived from its inner margin, is denser and less transparent and constitutes the **area opaca.** This, then, may be taken as the completion of the blastula stage although its formation and final appearance is quite unlike those of either *Amphioxus* or *Rana* owing to the enormous amount of yolk that is present in the ovum at the beginning.

Gastrulation or the differentiation of the two primary germ layers now takes place, but the method by which it is accomplished has not been satisfactorily determined in the case of the fowl, so that the account given here is based on the process as it occurs in the Pigeon. The area pellucida extends slowly and its increase is accompanied by a rearrangement of its cells, which finally become single layered towards the posterior end at which point they extend backwards forming a break in the germ ring. At this point a few of the cells on the edge turn in underneath and constitute the forerunners of the entoderm. This process increases in rate and extent and the place at which it takes place becomes a small, slightly raised crescentic ridge. Since this contains both ectoderm and entoderm cells, it can be regarded as the dorsal lip of the blastopore. These entoderm cells spread forwards and outwards under the ectoderm of the blastoderm and above the segmentation cavity in irregular groups and form a continuous sheet only at the hinder end. As a rule the egg is laid in this condition, *i.e.* with gastrulation not properly completed, and laying takes place twenty-one or twenty-two hours after ovulation. The blastoderm has increased slightly by this time and may measure as much as 5 mm. in diameter. It remains in this stage after it has been laid unless the temperature is raised either by its being placed under a sitting hen or in an incubator. These conditions induce **incubation** or a continuation of development outside the body of the parent. During the first few hours of incubation the formation of the entoderm is completed and the diploblastic condition established. In the same period also, we find that the ectoderm cells over the central region have become decidedly columnar, whereas towards the periphery they remain flat and so a thicker median area, the **embryonal shield,** is produced.

The formation of the third layer is heralded by the appearance of an opaque thicker band in the middle line of the hinder half of the blastoderm about nine hours after the beginning of incubation. This is the **primitive streak** and sections show that it is constituted at first by an aggregation of ectodermal cells in that region. With

the appearance of the streak the blastoderm begins to increase fairly rapidly, mainly by the extension of the area opaca equally in all directions. The streak itself also grows quickly in a posterior

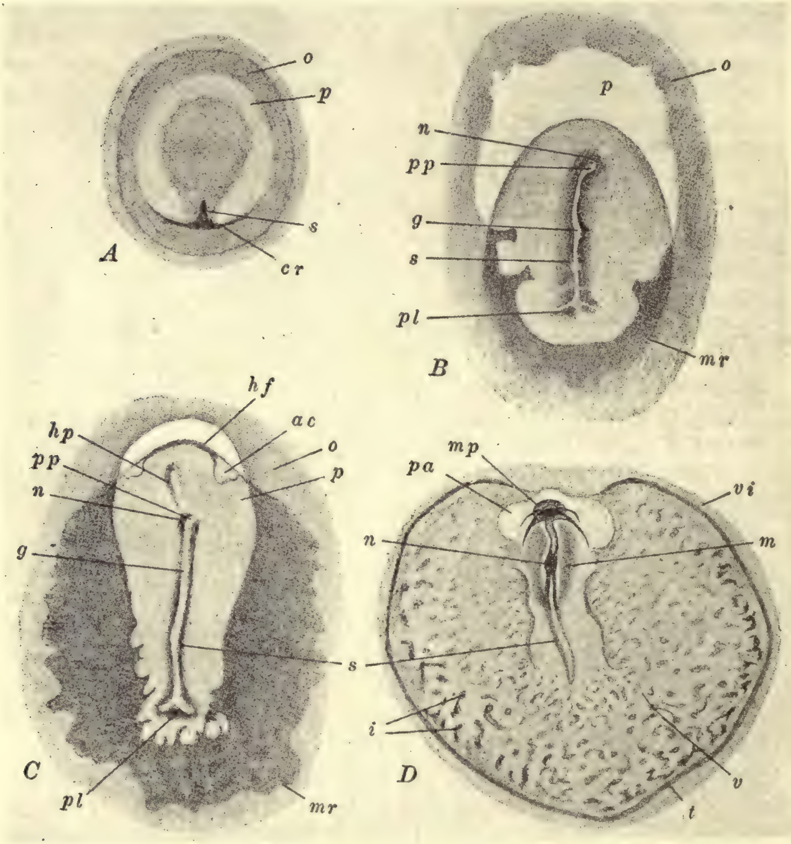


FIG. 138.—Chick blastoderms.—From Kellicott.

A, after Duval (modified); B–D, after Lillie. A, unincubated blastoderm, with primitive streak just forming. B, primitive streak formed, head process not yet indicated. C, head process formed; head-fold just commencing. D, just before the establishment of the first mesodermal somites. *ac*, amnio-cardiac vesicle; *cr*, crescent-shaped thickening at the posterior side of the blastoderm, in the region of entoderm and mesoderm formation; *g.*, primitive groove; *hf*, head fold; *hp*, head process; *i.*, blood islands; *m.*, axial thickening of mesoderm; *mp*, medullary plate; *mr*, margin of mesoderm; *n.*, Henson's node; *o.*, area opaca; *p.*, area pellucida; *pa*, proamnion; *pl*, primitive plate; *pp*, primitive pit; *s.*, primitive streak; *t.*, sinus terminalis (marginal sinus); *v.*, area vasculosa; *vi*, area vitellina interna.

direction its anterior end remaining relatively stationary. With this growth goes a lengthening of the area pellucida, which first becomes oval and later pear-shaped. As the primitive streak lengthens a superficial gutter-like depression, the **primitive groove,** appears

along the middle of it while its raised edges are known as the **primitive folds.** Its sides beneath the ectoderm are composed of actively proliferating cells which give off their products into the space between the ecto- and entoderm and so lay down the primitive mesoderm cells. The front end of the primitive streak thickens and swells out slightly to form the **primitive knot** or **Henson's knot,** and just behind it the primitive groove terminates in a slight depression the **primitive pit.** The mesoderm is given off very rapidly from the sides of the streak, passing out sideways, and it also aggregates in the middle line beneath the streak and there comes in contact with the underlying entoderm. This downward growth often makes it appear in section as if this portion of the mesoderm were derived from the entoderm. We have now reached a stage, then, in which the three primary germ layers have been definitely established and they are confined to the blastodermic area, being, as it were, unable to stretch round and encompass the yolk which occupies the position of the floor of the enteron.

However, this triploblastic condition has not yet brought the embryo up to the same stage of development as in *Amphioxus* and *Rana*, so that we may trace it a little further and, as up to the present there has been no indication of the appearance of a definite embryo, the immediately succeeding stages are often referred to as the period of formation or differentiation of the embryo.

The mesoderm, as we have seen, is produced by multiplication of the cells of the primitive streak ; indeed the streak itself is not really a definite structure, but merely the result of an active proliferation and consequent aggregation of cells along this line. This mesoderm spreads out laterally in the form of two wing-like plates which as they pass outwards, extend forward at their tips, and also finally these anterior lateral extensions turn inwards and meet in the middle line. Their front edges, therefore, run first outwards, then forwards, and finally inwards to meet well in front of the primitive knot, thus there is left an area between their union and the end of the primitive streak which is free of mesoderm and this region is termed the **proamnion.** By this time not only has the lateral plate of the mesoderm split into somatic and visceral layers, but in the latter have appeared a number of compact masses of cells that give this region of the blastoderm a characteristic mottled appearance. It is distinguished from the remaining parts of the blastoderm as the **area vasculosa,** since these masses, appearing as dark patches when the structure is viewed as a whole, are destined to give rise to the first blood-vessels and the blood itself. At a later stage the " blood islands," as they are first termed, extend and anastomose forming an interlacing series of blood-vessels over the whole of the area vasculosa.

By the time the primitive streak has reached its definitive size, a rod of cells, in surface view appearing very similar to the primitive streak, has started to grow forward from the primitive knot. This continues to grow at a slight angle to the line of the primitive streak until it passes just beyond the end of the embryonal shield, and as it is accompanied by mesoderm it pushes forward the hinder limit of the pro-amniotic area. It is often termed the **head process,** but is more suitably designated the **notochordal process** since it represents the beginning of the notochord. This process is actually an independent cellular strand growing forward from the knot, between the ectoderm and entoderm and most probably composed of cells derived from the latter layer, although of course at the knot itself it is in contact with all three layers. It should not be confused

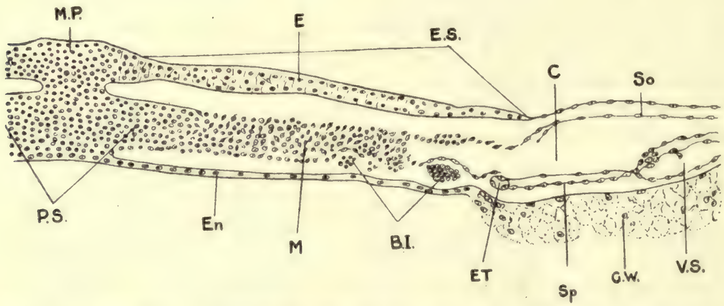


FIG. 139.—*Chick.* Transverse section of part of blastoderm in region of primitive streak in a chick with six pairs of somites (about twenty-four hours).—After Rückert.

B.I., blood islets; C., cœlom; E., ectoderm; En., entoderm; E.S., embryonal shield; E.T., endothelial tube; G.W., germ wall; M., mesoderm; M.P., medullary plate; P.S., primitive streak; So., somatic mesoderm; Sp., splanchnic mesoderm; V.S., vascular sinus.

with the primitive streak in spite of its somewhat similar superficial resemblance, as it is an entirely different structure and it marks definitely the axis of the future embryo.

As the notochordal process is growing forward an alteration occurs in the ectoderm of the embryonal shield lateral to it. It thickens to form the **medullary plate,** and this extends not merely along the sides of the notochord itself, but also lateral to the front end of the primitive streak. This plate is indicated in the beginning simply by a thickening of the shield and is flat save for the presence of the **dorsal groove,** a shallow median groove that brings the floor of the plate into contact with the notochordal process. Soon after its formation the extent of the plate becomes sharply defined by its edges rising up from the general level of the ectoderm to form the **neural** or **medullary folds.** When the folds become well developed

they transform the dorsal groove into a much wider and deeper **medullary groove.** At first the folds are lateral, but later they bend round in front to meet in the middle line, just behind the anterior border of the embryonal shield, and thus mark the limit of the medullary plate. Thus we have laid down the rudiment of the central nervous system.

A very important change occurs after the formation of the transverse neural fold, and that is the growth in this region becomes unequal. The fold itself rises up considerably above the level of the surrounding ectoderm, and then its dorsal region grows much more rapidly than its ventral part or than the front margin of the embryonal shield. It follows as a mechanical result from this that the transverse fold region begins to bend over and grow forward independently of and over the rest of the blastoderm. This overgrowth leads to the formation of a rounded process overlying the anterior end of the blastoderm in front of the notochordal process, a region which, it will be recalled, is the proamniotic area and contains no mesoderm. The folding produced in this way is known as the **head fold,** and it is the beginning of an important transformation. Up to the present, while there have been certain alterations in the thickness of its various parts, etc., the blastoderm has grown as a whole. Now, however, we find that a portion of it is becoming folded off from the rest and very sharply marked off from it. This process is known as **delimitation,** and we find later that the portion so folded off is destined to form the embryo, while the remaining part of the blastoderm takes no direct part in its formation, and is, in consequence, termed **extra-embryonic.** The growth of the head fold soon comes to involve both layers of the hinder part of the proamniotic area, and so in viewing the blastoderm from the surface, two rounded bay like formations facing in opposite directions can be distinguished. The uppermost of these is superficial, and lies between the shield ectoderm on the under side of the head fold and the extra embryonic ectoderm of the proamniotic area. It is known as the **head fold bay** and of course opens forwards on to the surface of the blastoderm. The other is a deeper-lying structure and is brought into being by the pulling forward and folding of the entoderm of this region with the extension of the head fold. This bay is enclosed by entoderm and opens backwards into the sub-germinal cavity. It is at first quite short, but nevertheless, an important structure, since it represents the **fore-gut** of the embryo. The relations of all these structures can be readily seen in a sagittal section.

When the head fold is commencing the mesoderm, as we have seen, covers a fairly extensive area, spreading out sideways from the primitive streak and notochordal process and it sweeps

forwards and inwards to leave the proamniotic area which is mesoderm free. As the head fold grows forwards a narrow band of the mesoderm situated along each side of the streak and notochord becomes thicker and more opaque than the remaining parts. This band is distinguished as the **vertebral plate, paraxial** or **segmental zone,** and the peripheral thinner sheet is termed the **lateral plate** or **parietal zone.** It has been pointed out also that the lateral sheet of mesoderm has already split to produce the cœlom which is therefore a schizocœl as in the frog. In the region just behind the head process the paraxial zone thins out and loses its definiteness, and certain of its cells migrate forward to form a loose network of cells in the fold itself, thus constituting the **mesenchyme** of the head, to which additions are made directly from the ectoderm of the head region. The great importance of the differentiation of the mesoderm is that the somites are derived from the paraxial zone, while the parietal zone is distributed to the rest of the embryo.

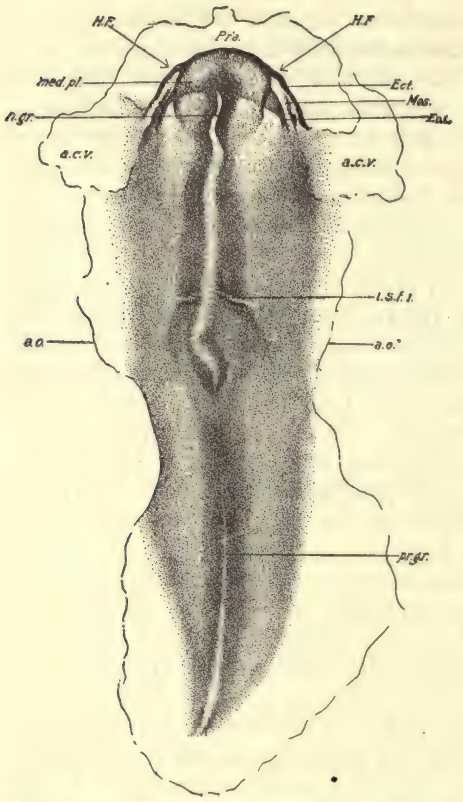


FIG. 140.—Chick, twenty-four hours.—From Lillie.

a.c.v., amnio-cardiac vesicle; *a.o.*, inner margin of area opaca; *ect.*, ectoderm; *ent.*, entoderm; *h.f.*, head fold; *i.s.f.l.*, first intersomitic furrow; *med.pl.*, medullary plate; *mes.*, mesoderm; *n.gr.*, neural groove; *pr.gr.*, primitive groove; *pr'a.*, proamnion.

About twenty hours after the beginning of incubation a pair of transverse furrows appear in the paraxial zone, a short distance in front of the primitive knot and the mesoderm immediately anterior to the furrow aggregates somewhat and forms an indistinct mass that can be considered as the first somite, although it is never clearly marked off from the rest of the front end of the zone. Shortly

afterwards the cells behind the furrows aggregate, and a second furrow appears sharply delimiting the second pair of the somites. From this time on the process of somite formation continues fairly regularly, each new pair being formed behind those preceding and the embryonic region grows at the expense of the primitive streak. It finally comes to an end on the fifth day of incubation, by which time fifty-two somites are formed. Not only is this number and order of formation constant, but the fate of the individual somites is also the same. The first pair of incomplete somites lie just behind the region where the ear will later develop, and the next three pairs with the former take part in the formation of the occipital region of the head. Although in lower forms like *Scyllium* segments are laid down in front of the auditory pit, this is not the case in the chick,

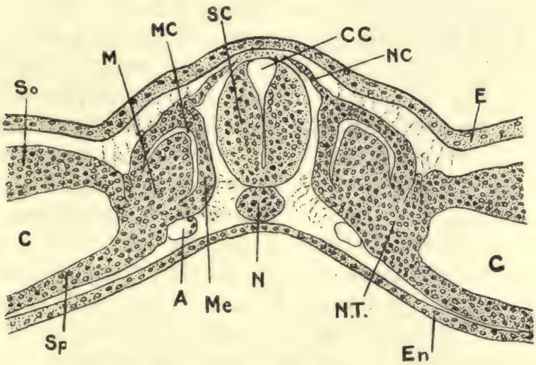


FIG. 141.—*Chick.* Transverse section through last somite of a chick with twenty-nine pairs of somites (about forty-eight hours').—Adapted from Lillie.

A., aorta ; C., cœlom ; C.C., canalis centralis ; E., ectoderm ; En., entoderm ; M., myotome ; M.C., myocœl ; Me., mesothelium ; N., notochord ; N.C., neural crest ; N.T., nephrotome ; S.C., spinal cord ; So., somatic mesoderm ; Sp., splanchnic mesoderm.

and there is no indication of segmentation in front of the ear. The mesodermal somites therefore express very clearly the primitive metamerically segmented condition of the body, which is hidden to a large extent in the adult. As the rate of incubation varies with different conditions and individuals, it is often the custom to distinguish the stage of development reached by the number of somites present rather than by the number of hours of incubation.

A transverse section shows clearly the relation between the two regions of mesoderm. The outer cells of the somite are seen to be arranged in a fairly definite layer, the **mesothelium,** around a more central mass. Between these two divisions is a very narrow

curved slit, the **myocœl ;** as a matter of fact it is more potential than actual in the chick. The somite, then, is a more or less clearly marked oblong mass of cells having a definite arrangement. It is joined on to the parietal mesoderm, between whose somatic and splanchnic layers there is by this time a fairly large cœlomic space, by a narrow strip of cells variously known as the **intermediate cell mass,** the **somitic stalk** or **nephrotome.** The last name is applied to indicate that this small portion is destined in the main to give rise to the excretory system, but a part of it also contributes to the formation of the mesenchyme.

It is now necessary to return again to the central nervous system, whose beginning we have already noted in the medullary plate. Practically the whole of this structure in front of the primitive knot is destined to take part in the formation of the brain and is consequently sometimes distinguished as the **brain plate.** The medullary folds gradually get higher and higher, and the medullary groove in consequence deeper and also narrower. Finally the folds turn inwards and grow towards the middle line, where they meet and fuse, thus converting the plate into the **neural tube** and the groove into the **neural canal.** They meet first at a point a little way back from the front end of the head fold in a region that will give rise later to the mid-brain. Before the actual fusion has taken place, however, it will be noticed that the folds at the anterior end are much deeper and more strongly marked than posteriorly, consequently the neural tube when formed is markedly larger in front than behind. This swelling forecasts the division between the brain and spinal cord regions of the central nervous system. The two are not sharply demarked and pass insensibly into one another. We have already noted that the first four pairs of somites are included in the head of the adult, and therefore the hinder limit of the fourth pair may be taken as marking the end of the brain and beginning of the spinal cord.

From the very first the brain is much larger than the cord, and even in a chick of 33 hours' incubation (*i.e.* with twelve pairs of somites), it occupies more than half the total length of the neural area, a precocious development apparently necessitated by the relatively large size of the brain when fully grown. In the embryo of 24 hours, before the fusion of the folds, another specialisation has made its appearance, and that is that the front end of the folds is marked off by a distinct constriction, while the hinder parts of the folds simply decrease uniformly as they pass backwards. The first point of fusion is behind this constriction, and from it the union extends forwards slowly, leaving a small aperture, the **neuropore,** for some while right at its front end. The lips of this opening when they fuse

give rise to the **lamina terminalis.** The fusion of the neural folds proceeds more rapidly in the posterior direction, although the extreme hinder ends remain apart for a considerable time, and as it does so a second constriction forms. The first constriction marks off the **fore-brain** vesicle or **prosencephalon,** and the second, the **mid-brain vesicle** or **mesencephalon,** while the remaining part of the brain region is termed the **hind-brain vesicle** or **rhombencephalon.** Even at this early stage the ventro-lateral walls of the fore-brain have bulged out laterally to form the rudiments of the optic vesicles. Closer examination shows that underlying this primary division of the brain there is an indication of segmentation, so that the brain itself may be regarded as consisting of a series of segments or **neuromeres,** marked off from one another by faint constrictions. Three such neuromeres are generally held to be present in the fore-brain, two in the mid-brain, and in the hind-brain five can fairly easily be distinguished, of which the hindermost is the largest and usually considered to represent two. The total number of neuromeres in the chick therefore is eleven.

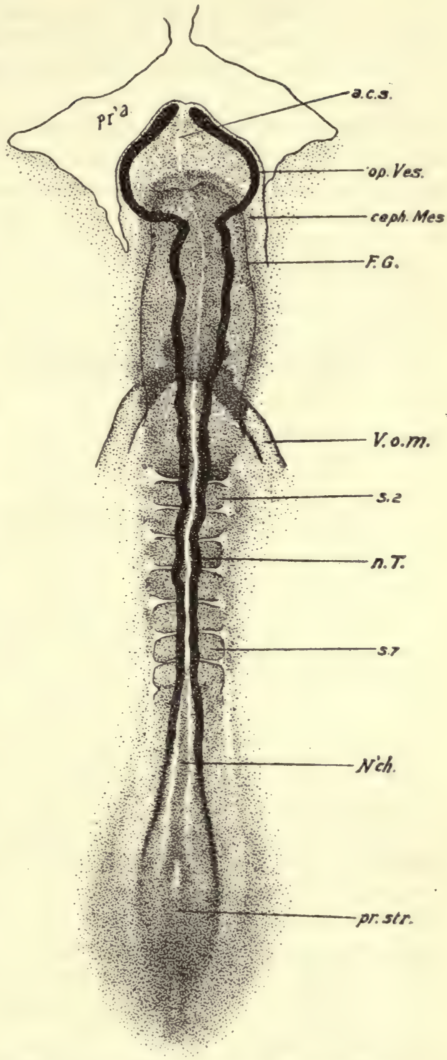


FIG. 142.—Chick, seven pairs somites.—From Lillie.

a.c.s., anterior cerebral suture ; *ceph.Mes.*, cephalic mesoblast ; *F.G.*, fore-gut ; *N'ch.*, notochord ; *n.T.*, neural tube ; *op.Ves.*, optic vesicle ; *pr'a.*, proamnion ; *pr.str.*, primitive streak ; *s2.*, *s7.*, second and seventh somites ; *V.o.m.*, omphalo-mesenteric vein.

The tops of the neural folds as they come together are somewhat flattened, so that when they join, a portion of the nervous matter is left under the superficial ectoderm along the sides of the line of junction. This does not take part in the formation of the tube itself, but is left as a pair of longitudinal bands on the dorso-lateral sides of the neural tube. These are the **neural crests,** and will give rise to the ganglia of the cranial and spinal nerves.

We have thus followed the development of the chick up to a stage corresponding fairly closely with those at which we left *Amphioxus* and *Rana*, and in spite of the considerable differences in the method of attaining it, owing to the presence of a large amount of yolk, the condition of the embryo in all three species shows a remarkable fundamental resemblance.

Lepus.

The study of the development of the mammalian ovum is one that presents a number of difficulties. In the first place the ovum itself is of small size, being about ·2 mm. in diameter in man and ·17 mm. in the dog and the rabbit; this makes it hard to find and manipulate when obtained. Secondly, save in the case of the rabbit, there is no definite relationship between ovulation and any external happening, so that it is largely a matter of chance if early stages are obtained. In the rabbit ovulation occurs 9 or 10 hours after copulation, so that in this species one difficulty is partly removed. Then, too, the mammalian egg has undoubtedly been derived from a large heavily yolked telolecithal egg, somewhat like that of the fowl. In spite of its small size and the fact that it is almost devoid of yolk, it follows in its development the same general course as a telolecithal egg and does not return to the primitive homolecithal type. Lastly, the segmenting ovum, deprived of yolk as source of food supply, takes on, at quite an early stage, a definite and very intimate connection with the wall of the uterus, whence it obtains its nutriment. This profoundly modifies the early stages of development, and so we find a number of processes occurring, particularly in the early stages of segmentation, that either have no counterpart in other forms or else our knowledge of them is insufficient to allow of definite homologies being established.

The extrusion of the first polar body occurs while the ovum is still in the graafian follicle. When the latter has become fully formed, it slowly enlarges until it is transformed into a hollow vesicle filled with follicular fluid and having its walls lined by a layer several cells thick, the **membrana granulosa.** To one side of this the ovum is attached by means of a group of cells surrounding it.

When the follicle is fully ripe in most mammals it ruptures spontaneously at a time that is associated with a general physiological condition known as **heat** or **œstrus.** In the rabbit, as noted, the ripe follicle does not burst until after copulation, which occurs during œstrus. The ovum thus released is received by the oviducal funnel, and at the top of the oviduct it is fertilised by the entrance of a single sperm. This is followed by the formation and extrusion of the second polar body.

The egg when it leaves the follicle is a minute spherical cell composed of semi-transparent protoplasm, and it contains a vesicular nucleus with little chromatin but a well-marked karyosome. A few yolk spheres may be present, but never many. It is surrounded by an egg membrane, perhaps a secondary egg membrane, which is termed the **zona pellucida.** This is frequently striated for part or the whole of its thickness, suggesting that it is perforated by minute canals, and so this region is sometimes called the **zona radiata.**

The first cleavage is complete cutting the ovum into two equal or approximately equal cells. The second cleavage is also complete and generally simultaneous in the first two cells, and the four resultant daughter cells are usually arranged in a characteristic cross. After this the segmentation is more or less irregular, and as a result of it there is produced a small solid mass of cells, the **morula.** At quite an early stage a certain amount of organisation can be distinguished in this morula, for it will be seen that the outer cells form a definite peripheral layer around a more irregular internal group. As these changes occur while the egg is still surrounded by the zona, the superficial layer is termed the **sub-zonal layer** and the remainder the **internal cell mass.** As segmentation continues a cleft appears between the two groups of cells, and it enlarges until the internal cell mass is separated from the sub-zona layer by a fluid-filled cavity, save at one point where they remain in contact. Thus we have a hollow sphere with a wall one cell thick, the **blastodermic vesicle,** supporting within it at its upper pole the inner cell mass. Its cavity is taken to represent the yolk mass of an egg, like that of the fowl. That is to say, the cavity is the subgerminal cavity extended to include the whole of a hypothetical yolk mass, which is replaced by a small amount of fluid. The vesicle wall is regarded as ectodermal, but since it takes no part in the actual formation of the embryo it must be regarded as corresponding to the extra-embryonal ectoderm of the chick. By the time this stage has been reached the egg has traversed the Fallopian tube and lies in the uterine cavity, and since the vesicle wall is the part brought into contact with the uterus it is obvious that it will be

the portion to be modified in connection with fixation and nutritive requirements of the embryo. After reaching the uterus the blastodermic vesicle enlarges fairly rapidly and in some species may reach quite a large size. As its wall later takes part in the formation of the **placenta,** which is among other things an organ of nutrition, it comes to be termed the **trophoblast** or **trophoblastic ectoderm.** The remaining internal group of cells, which is responsible for the

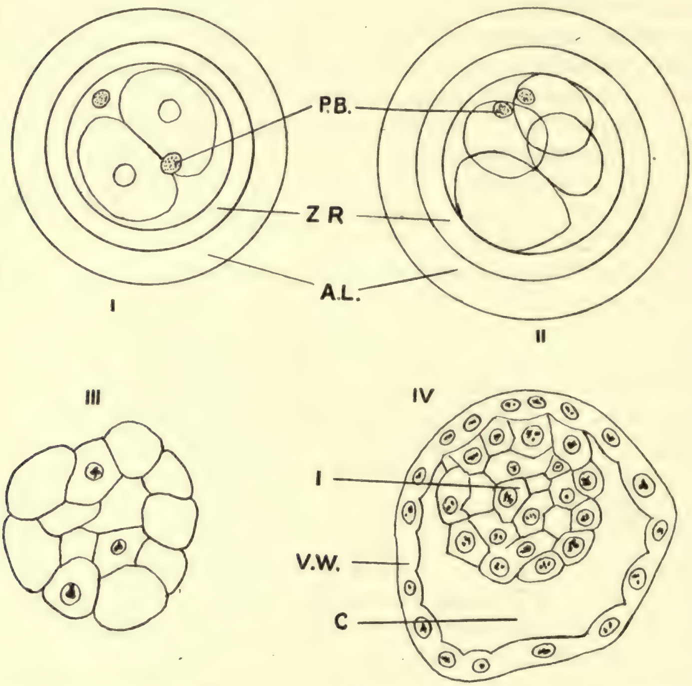


FIG. 143.—*Lepus*. Segmentation of egg of rabbit. I. and II., first and second cleavages; III., section through morula; IV., section through fairly advanced blastodermic vesicle.—After Assheton.

A.L., albuminous layer; C., cavity of blastoderm; I., inner cell mass; P.B., polar body; V.W., wall of blastodermic vesicle; Z.R., zona radiata.

production of the entire embryo and the whole entoderm, both intra- and extra-embryonal, is distinguished from the former as the **formative** or **embryonal ectoderm.**

Two important processes now go on simultaneously, namely, the formation of the germ layers and the embryonic rudiment, and secondly the implantation or embedding of the vesicle in the uterine wall. For convenience these two processes will be considered

separately, and indeed, since the implantation is intimately connected with certain covering embryonic membranes that are produced in the course of development, its consideration will be held over until we have followed the growth of similar membranes in the chick. It should be borne in mind, however, that this division is purely artificial and the changes go on side by side.

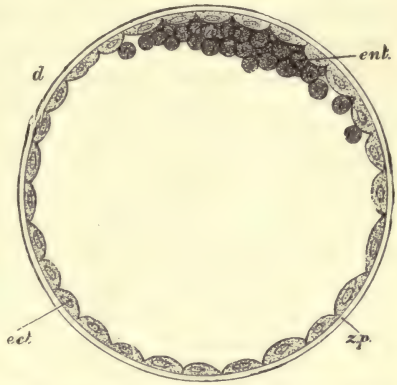


FIG. 144.—Rabbit, blastocyst.—From Quain.

ect., trophoblastic ectoderm ; *ent.*, inner cell mass ; *z.p.*, zona pellucida.

During the subsequent growth the internal cell mass flattens and spreads out until it forms a thin disc underlying the trophoblast at one pole ; the mass, however, soon becomes differentiated into two layers. The outer layer is the **ectoderm,** and its cells multiply rapidly and become cubical, and in this way give rise to the ectoderm of the definitive **embryonal shield.** The lower layer cells form the **entoderm** ; they flatten out and grow rapidly and in typical cases spread completely round the inside of the blastocyst, which is thus made bilaminar. This, then, concludes the process of gastrulation or formation of the two primary germ layers. At first, in all cases, the inner cell mass is covered by a layer of trophoblastic, often referred to as **Rauber's layer.** Thus over this area the blastocyst is trilaminar. The blastocyst as a whole continues to grow during this period, and is kept turgid by the infiltration of a fluid produced by a series of glands in the uterine wall.

The fate of Rauber's layer is not the same in different groups, and the transformations in its neighbourhood may be complex. In the bats, many rodents and perhaps man, this layer persists and becomes separated from the embryonal shield by a cavity designated the **primitive amniotic cavity,** since it is destined later to give rise to the true amniotic cavity. In other species, notably the rabbit, it appears as if the rapid growth of the embryonal shield, which fuses with the trophoblast around its edges, stretches the layer until it breaks down into a number of loose cells lying under the zona and between it and the shield. These cells may, perhaps, merge in the ectoderm of the shield, but at any rate they disappear as separate structures, and so the blastocyst becomes bilaminar throughout. It will be clear, however, that while the greater part of its periphery is

composed of the retained trophoblastic ectoderm plus the entoderm, a circular area is formed of embryonal ecto and entoderm. In other words, then, in this form the embryonal ectoderm becomes exposed on the surface of the blastocyst. Embryos of this type also develop an amnion, but later and by means of the overgrowth of folds much in the same way as in the chick, as we shall see below.

The embryonal shield now grows and becomes first oval and then pear-shaped. While it is still oval a primitive streak and primitive knot make their appearance almost simultaneously as an opaque line and spot occupying the posterior two-thirds of the shield. A primitive groove also appears, and about the same time a less obvious dark line running forwards from the knot indicates the presence of a notochordal process. All these structures recall the similar ones in the chick, which they resemble in origin and structure. The primitive streak is the result of the active proliferation of the ectodermal cells along a median line, and the cells budded off from it become arranged to form a layer between ecto- and entoderm. As in the chick, then, the mesoderm is ectodermal in origin. The primitive knot in the mammal is slightly different from that in the chick. In the first place the entoderm is not firmly united to it on the under side, and, secondly, it may have a perforation which leads to a small cavity in the notochordal process known as the **notochordal canal.** This structure, while not appearing in the chick, is characteristic of certain Reptiles. In the rabbit, however, this canal is only represented by a groove on the lower surface of the shield.

It is not necessary to go into the details of succeeding stages of development, since they resemble those of the chick fairly closely. A medullary plate is formed whose edges bend up as medullary folds and finally fuse in the middle line to form a neural tube whose primary brain vesicles are already indicated before the union of the folds. The mesoderm sheet spreads out and soon passes out into the extra-embryonal regions. Paraxial bands develop in it, and segment into typical mesoblastic somites. The cœlom appears as a split separating the mesoderm into somatic and splanchnic layers, and is divisible into a myocœl and splanchnocœl.

With this we may conclude the account of the early development of the fertilised ovum in four distinct types, *Amphioxus*, *Rana*, *Gallus* and a Mammal, *Lepus*. In spite of the great differences due to the particular conditions under which each individually develops, there is a still greater fundamental similarity which is all the more striking since it is exhibited under such diverse conditions.

CHAPTER XVI

LATER DEVELOPMENT OF CHICK AND RABBIT

Chick.

Vascular System.

As we have noted already, even before the somites have been formed, an **area vasculosa** is marked out in the area opaca, and it appears in surface view as a mottled region. This spreads fairly rapidly, and by 38 hours completely covers the embryonic area, having around its edge a continuous dark line. These patches, which, it should be noted, are extra embryonal and outside the area pellucida, are actually closely packed irregular groups of cells lying between the meso and entoderm, and receive the name of "blood islands." They soon connect up and form an anastomising network. In the stage when three or four somites are laid down, vacuoles appear in these groups, and the outer cells arrange themselves in a flattened layer to form the endothelium of the future blood-vessels, while the remaining cells round off and develop hæmoglobin, thus forming the **erythrocytes** or first blood cells. So that around the periphery of the area where a similar process goes on a continuous limiting vessel, the **sinus terminalis,** is formed, and all over the remaining parts a network of capillaries in which larger trunks soon appear. These include the **anterior vitelline veins** running from the anterior margin of the area vasculosa backwards, and the **lateral vitelline veins** coming in from the side. The vessels thus formed invade, at quite an early stage, the area pellucida, which never possesses distinct blood islands. As the lateral mesoderm splits it will be found that the vessels are confined to the splanchnic layer, while the somatic layer is non-vascular.

The first embryonal vessels to appear are the **dorsal aortæ,** a pair of tubular structures lying in the mesoderm latero-ventrally to the neural tube. They pass forward to the head region, and posteriorly they diverge at about the level of the last somite in an embryo of 12 somites, to run out into the vascular area as the **vitelline arteries.**

As the head fold is forming, the cœlom just behind it enlarges markedly to form a pair of sacs, the **amnio-cardiac vesicles.** These

grow inwards towards the middle line between the ecto- and entoderm layers, thus making the gut wall at this point very deep. The second vessels to appear are a pair of **ventral aortæ,** beneath and ventral to the fore gut, and these run backwards and pass out behind the opening leading into the fore gut, *i.e.* the **anterior intestinal portal,** into the vascular network as the vitelline veins. These two thin tubes run along the inner side of the vertical portion of mesoderm of the mesial walls of the amnio-cardiac vesicles, whose walls are thickened in this region to form the **myocardium,** which is destined to give rise to the main mass of the muscles of the heart. Very soon after, the vesicles fuse in the middle line to form a median space, the future pericardium, and the two endothelial tubes also fuse over part of their length to form a single vessel, the **endocardium,** which provides the lining of the various chambers of the heart. The fusion of the vesicles forces the anterior intestinal portal backwards. The heart rudiment then comes to be a median tube continuous with two posterior limbs diverging as the vitelline veins, and passing forwards into the two ventral aortæ, which communicate around the front end of the fore gut with the dorsal aortæ by connecting trunks termed the first or **mandibular arches.**

The heart tube itself increases in length, but as its anterior and posterior ends are relatively fixed, the enlargement results in a bulging out to the right side, and so allows two divisions to be recognised, an anterior **ventricular portion** and a posterior **atrial portion.** To the hinder end a further region, the **sinus venosus,** is added by a fusion of a part of the vitelline veins. Further growth leads to a still more pronounced bending, and the ventricular region, the anterior end of which is by this time differentiated to form a **bulbus arteriosus,** gradually moves down ventral to the atrial region, ultimately coming to lie behind it. Next the atrium is divided into two by the growth of the **inter-atrial septum,** and a union and enlargement of the proximal ends of the vitelline veins forms the sinus venosus. Finally, the bulbar portion becomes absorbed into the right side of the ventricle, so that with the division of the ventricle into two, as a result of the development of the **interventricular septum,** the bulbus arteriosus comes to be incorporated with the right ventricle only.

As noted previously, at the thirtieth hour the dorsal and ventral aortæ are united by but a single arch on each side, but during the second day, firstly, the **second** or **hyoid arch** is formed and then a **third arch.** By the end of the third day a **fourth arch** has been completed, and the **fifth** and **sixth arches** are established during the fourth and fifth days. Of these arches the fourth and sixth are most strongly marked, while the fifth is only transitory and incomplete.

The adult condition is reached as a result of the disappearance of the whole fifth arch, the proximal parts of the first and second arches, and certain of the connecting vessels. The presence of the six arterial arches passing round the pharynx in relation to rudimentary gill clefts is characteristic of all vertebrates from Amphibia up, and recalls the condition that obtains permanently in the adult fish. In all these higher groups, too, the same arches persist throughout life, and practically the same portions are lost or cease to function.

The first embryonal veins to appear, during the second day,

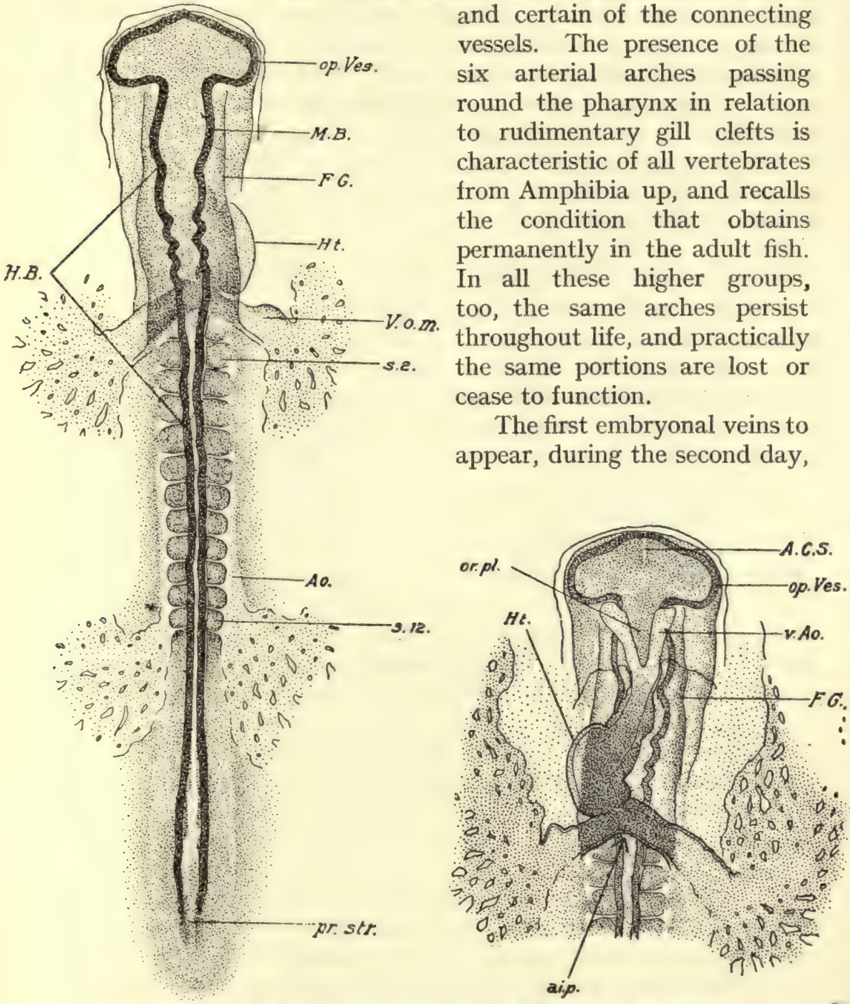


FIG. 145.—Chick, twelve pairs somites (33 hours).—From Lillie.

H.B., hind-brain; *op.Ves.*, optic vesicle; *M.B.*, mid-brain; *F.G.*, fore-gut; *Ht.*, heart; *V.o.m.*, omphalo-mesenteric vein; *s2.*, *s12.*, second and twelfth somites; *Ao.*, aorta.; *pr.str.*, primitive streak; *or.pl.*, oral plate; *A.C.S.*, anterior cerebral suture; *v.Ao.*, ventral aorta; *ai.p.*, anterior intestinal portal.

are the **anterior cardinal veins,** a pair of vessels running back along the ventro-lateral walls of the brain, each receiving an external jugular vein from the floor of the pharynx. Proximally they enlarge and

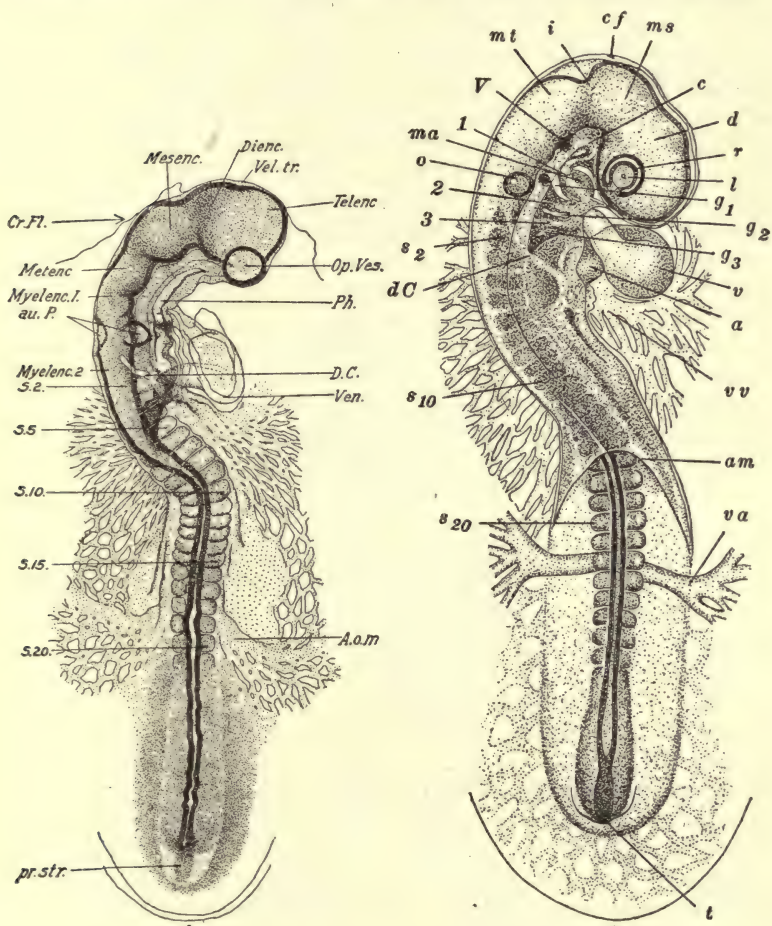
turn inwards to form the two **ducti Cuvieri,** which enter the sinus venosus, one on each side. The **posterior cardinal vein** arises as an outgrowth from the ductus Cuvieri and passes backwards laterally to the somites and above the intermediate cell mass to the tail. At a later stage the two lateral vitelline veins unite to form a single vessel, the **ductus venosus** or **main splanchnic vein,** opening into the posterior end of the sinus venosus. The two anterior vitelline veins fuse near the sinus terminalis and the right vein then disappears, leaving the left to open into the posterior end of the heart.

Delimitation of the Embryo.

The manner in which the head end of the embryo grows off the blastoderm as a head fold has already been discussed, and it was noted that it produced a head fold bay, which may appropriately be termed the **anterior limiting sulcus,** since it separates the anterior end of the embryo from the blastoderm. This general embryonic growth, early marked at the front end, goes on somewhat more slowly over the whole embryo in length, breadth and thickness. After the eighteenth pair of somites have been formed, the primitive streak as such disappears, and is represented only as an area of active cell proliferation, the **tail bud.** By the time twenty-six somite pairs are established, *i.e.* about 46 hours, this point grows off the blastoderm in a similar manner to the head, thus bringing into being a **tail fold** and a **posterior limiting sulcus.** This growth involves also the entoderm, giving rise to a **hind gut.** The intervening part of the embryo, too, has been getting thicker, and so rising above the blastoderm, and a little later, as this upstanding part widens, we have produced the **lateral limiting sulci,** connecting up the anterior and posterior sulci. In this manner, then, the actual embryo becomes sharply marked off from the surrounding blastoderm by an encircling groove.

Thus, from being just a thickening in the middle region of the blastoderm, and passing out insensibly into the extra-embryonal region, the embryo becomes a sharply delimited structure. Even before this marking off is complete general changes have been taking place in the conformation of the embryo as a whole that need to be considered before passing on. Up to the stage where twleve pairs of somites are present (about 33 hours) the axis of the embryo is fairly straight, but when 15 somites have appeared (about 36 hours) it will be noted that the head end is turning definitely to the right; the bend, or **cranial flexure,** is brought about by the rapid growth of the roof of the mid-brain. The turning is not due to the left side growing faster than the right, but to the combined twisting and

bending of the front end of the embryo in such a manner that not



A B

FIG. 146.—A. Chick embryo with twenty pairs of somites (45 hours), dorsal view. B. Chick embryo with twenty-seven pairs of somites (48 hours), viewed from above.—From Kellicott, after Lillie.

A. *A.o.m.*, vitelline artery ; *au.P.*, auditory pit ; *Cr.Fl.*, cranial flexure ; *D.C.*, ductus Cuvieri ; *Dienc.*, diencephalon ; *mesenc.*, mesencephalon ; *Metenc.*, metencephalon ; *Myelenc.*, 1 and 2, anterior and posterior divisions of the myelencephalon ; *Op.Ves.*, optic vesicle ; *Ph.*, pharynx ; *pr.str.*, primitive streak ; *s2*, *s5*, etc., second, fifth, etc., somites ; *Telenc.*, telencephalon ; *Vel.tr.*, velum transversum ; *Ven.*, ventricle.

B. *a.*, auricle ; *am.*, posterior margin of amnionic folds ; *c.*, carotid loop ; *cf.*, cranial flexure ; *d.*, diencephalon ; *d.C.*, ductus Cuvieri ; *g1*, *g2*, *g3*, first, second, and third gill clefts ; *i.*, isthmus ; *l.*, lens ; *ma.*, mandibular arch ; *ms.*, mesencephalon ; *mt.*, metencephalon ; *o.*, otocyst (auditory sac) ; just to the right of the otocyst is a thickening representing the ganglion of the VII. and VIII. cranial nerves ; *r.*, retinal layer ; *s2*, *s10*, *s20*, second, tenth, and twentieth somites ; *t.*, tail-bud ; *v.*, ventricle ; *v.a.*, vitelline artery ; *v.v.*, vitelline vein ; 1, 2, 3, first, second, and third aortic arches ; *V.*, ganglion of V. cranial nerve.

only does the anterior end turn to the right, but the right side of the

head turns uppermost and the left side downwards. It is probably a mechanical result of the cranial flexure, for the head is unable to bend straight downwards, owing to the presence of the yolk. At the stage of 20 somites (about 43 hours) this is very clearly marked. Five hours later (27 somites) another bend has made its appearance, this is the **cervical flexure,** and is produced by the increased growth of the roof of the hind-brain, causing a curving of the whole hind-brain region. The result of these two flexures and the enlargement of the fore-brain vesicle is that the front end of the head becomes directed backwards and finally inwards also. The maximum amount of bending is reached in the stage of 35 pairs of somites (about 72 hours). The appearance of the actively growing tail-bud leads to a similar but much less extensive bending of the small posterior end of the embryo. This also turns to the right, and is well marked at 72 hours. Indeed, the whole embryo tends to turn in the same direction, save in the region of the vitelline veins, so that it comes to lie nearly on its left side, and the heart also becomes displaced to the right.

Fœtal Membranes.

The fœtal membranes are four in number, viz.: the amnion, the chorion, the yolk-sac and the allantois. The first three of these are produced by the extra-embryonal blastoderm, while the last is an actual outgrowth from the body of the embryo itself.

The first two are developed together as the result of one process, and we may commence with them. The actual details of their formation are somewhat complicated, but it will suffice if only the general outlines are considered. Their formation is initiated in a chick about 30 hours old by the appearance of a transverse ridge across the pro-amniotic area in front of the head. This increases in height, and a section across it shows that originally it involves the ectoderm and the entoderm; at a later stage, however, the mesoderm and cœlom invade this area, and so the fold ultimately involves only the ectoderm and the somatic mesoderm, while the entoderm, with its accompanying splanchnic mesoderm, sinks back again to a lower level. The **head fold of the amnion,** as this ridge is termed, assumes a crescentic shape, and its ends pass back as the lateral amniotic folds. The fold gets higher and grows back fairly rapidly, completely enclosing the head, and at 48 hours (26–28 somites) has reached back almost to the level of the vitelline veins. At this time a **tail fold of the amnion appears,** similar to the anterior one, save that it consists of ectoderm and somatic mesoderm from the very commencement, and never involves the entoderm. Its lateral folds join up with the pre-existing ones, so that the whole embryo is

covered save for a long oval opening towards the hinder end. This gradually narrows down, and is completely closed up by the end of the third day of incubation. As the folds meet over the embryo the junction between them breaks down save over a limited area, where it persists, and their constituent layers fuse. Thus it comes about that the embryo becomes covered superficially by two very thin membranes. The innermost of these is the **amnion,** and it is composed of a layer of ectoderm continuous with the embryonal ectoderm on the inside and a layer of somatic mesoderm on the outside. The embryo itself then comes to lie in the floor of a hollow cavity, the

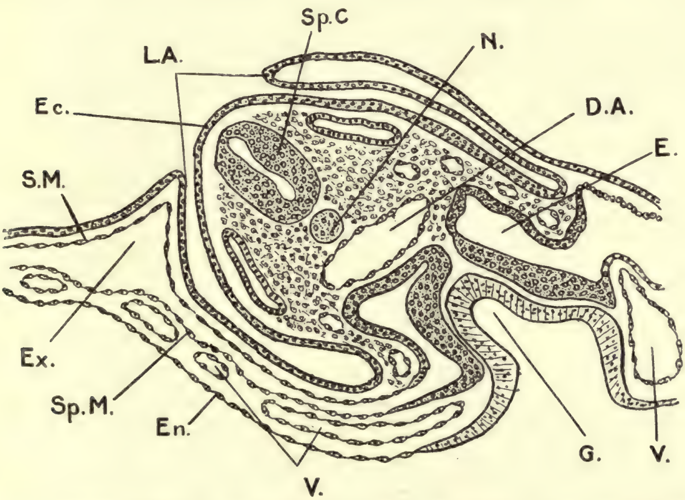


FIG. 147.—Chick embryo. Transverse section of embryo with twenty-eight pairs of somites (about 48 hours) in region where grit remains open.—Adapted from Duval.

D.A., dorsal aorta; E., embryonic cœlom; Ec., ectoderm; En., entoderm; Ex., exocœl; G., enteric groove; L.A., lateral amniotic folds; N., notochord; S.M., somatic mesoderm; Sp.C., spinal cord; Sp.M., splanchnic mesoderm; V., vitelline veins.

amniotic cavity, which becomes filled with a clear liquid, the **amniotic fluid.** Outside this, and separated from it by an extension of the extra-embryonic cœlom, is the second layer, the **chorion** or false amnion. This is composed of the somatic mesoderm, internally and externally, by ectoderm continuous with the general extra-embryonic ectoderm. It has been noted that along the line marking the final point of closure of the amniotic folds the junction between them does not break down. The folds remain firmly united in this region, which is termed the **sero-amniotic connection,** and this affects the future arrangements of the membranes to a considerable extent.

In a previous chapter the manner in which the blastoderm spreads out over the yolk has been described, and this expansion has been going on at the same time as the above phenomenon. The result is that the ring of peripheral periblast, with its accompanying sinus terminalis, has passed a good way round the yolk by the time the formation of the amnion is completed. The actual growing edge is formed by the union of ecto- and entoderm, but it is closely followed by the mesoderm, which splits as it progresses into splanchnic and somatic layers separated by extra-embryonal cœlom. This process is not completed until the twelfth day, and then, as will be realised, the yolk will be enclosed in a bag composed on the inside of entoderm and on the outside of splanchnic mesoderm. The **yolk sac,** as this structure is called, is separated from the outside layer of the blastoderm, composed of ectoderm and somatic mesoderm, by the extra-embryonic cœlom. Long before the completion of this process this layer over the yolk, the splanchnic mesoderm and entoderm, or **splanchnopleure,** is spoken of as the yolk sac, and from its walls a series of unfoldings, the yolk sac septa, arise. At first its connection with the embryonic gut is a wide one, but it gradually becomes restricted with the formation of the limiting sulci, the fore and hind guts, and the fusion of the amnio-cardiac vesicles. Independently of these, however, the splanchnopleure continues to constrict, until finally it is reduced to a narrow tube, the **yolk stalk,** putting the cavity of the sac in communication with the lumen of the gut in the region of the vitelline veins. Somewhat later the limiting sulci, *i.e.* the somatopleure, composed of ectoderm and somatic mesoderm, also constricts, until it leaves only a narrow opening, the **umbilicus,** around the yolk stalk.

The **allantois** is entirely different from the other membranes we have discussed, inasmuch as it is of embryonal origin. We have seen that the tail fold brings with it the formation of a short hind gut, which later becomes lengthened, not only by direct growth, but also by the processes resulting in the formation of the yolk stalk and umbilicus. At an early stage a ventral depression appears in the floor of the hind gut, and this grows outwards as a tubular structure from the tail fold bay into the extra-embryonal cœlom. It has just commenced to do this by the end of the third day. It will be noticed that from the beginning it is composed of entoderm internally, ectoderm externally, and mesoderm between them: the latter being continuous with the somatic mesoderm of the embryo. After a short while the outgrowth develops a characteristic arrangement of blood-vessels. Later, the proximal part of this outgrowth, which remains narrow, is termed the **allantoic stalk,** while the distal portion reaches the chorion and spreads out to form an enormous

flattened sac, which by the twelfth day has spread almost entirely around the blastoderm. It fuses with the chorion to form a combined structure, the **allanto-chorion.** This is a very important organ in the physiological life of the actively growing embryo. The circulatory system of this organ is composed of two large allantoic arteries and one large allantoic vein connected by a complicated plexus of anastomosing vessels. The allanto-chorion receives the nitrogenous excretion of the embryo, is the organ of respiration, and also greatly assists in the absorption of the albuminous white of the egg.

Gut and Related Structures.

In the formation of the gut three regions can be distinguished: the first is the fore gut, formed, as we have seen, by the pulling in of the entoderm during the formation of the head fold; the second in order of formation is the hind gut, resulting from the formation of the tail fold; and the third is the mid gut, which joins the two preceding portions, and is completed by the closing in of the splanchnopleure all along, save at the yolk sac opening. The first two are the most important.

As the head fold forms, the ectoderm on its underside bends up, touches and fuses with the entoderm of the front end of the fore gut to form the **oral plate.** This is at first superficial, but, with the flexure of the front end of the embryo, it becomes overhung by a ridge, and shortly after the mesoderm at its sides thickens to form two ridges, the mandibular arches, and so the plate comes to lie at the bottom of a shallow depression, the **oral fossa** or **stomodœum.** At the beginning of the third day the oral plate ruptures, putting the lumen of the fore gut in communication with the stomodœum. Even before this time the dorsal stomodœal wall gives off an outgrowth that grows in under the floor of the fore-brain, and later its terminal portion becomes detached and forms the glandular portion of the hypophysis cerebri. The formation of the jaws greatly enlarges the stomodœum, which gives rise to the buccal cavity of the adult, and hence the latter is lined by ectoderm.

From the fore gut arise the pharynx with the branchial pouches, lungs, œsophagus, stomach, duodenum, liver and pancreas. The front end of the gut is the pharyngeal region, and along four transverse lines on each side it bulges to form a series of grooves, the **visceral** or **branchial pouches.** The first of these to appear is the **hyomandibular pouch,** which is noticeable at 38 hours (14–16 somites) as a groove on each side just in front of the level of the auditory pits. Its deeper portion reaches and fuses with the ectoderm to form a branchial membrane. The second pouch appears at

43 hours (19–20 somites), and the third and fourth at 45 hours (23 somites) and 3 days (35 somites) respectively, and in each case a branchial membrane is formed. Externally the ectoderm opposite each pouch becomes grooved inwards, constituting the ectodermal moiety of the pouch and the membranes of all save the fourth break-down for a while, thus giving rise to three transitory **visceral clefts.** Between the pouches the mesenchyme thickens to form the **visceral arches,** of which five can be recognised. Of these, the first or mandibular arch lies in front of the hyomandibular pouch, and the second arch, between this cleft and the next, is the **hyoid arch.** In these arches develop a vascular system, composed of afferent and efferent vessels, and the rudiments of skeletal supports, so that we have produced a pharyngeal complex characteristic of a water-dwelling Vertebrate. The mandibular arches extend downwards, uniting in the middle line, and their skeletal elements give rise to the lower jaws.

The visceral pouches have but a short existence, and finally disappear, save for certain remnants. The dorsal region of the hyomandibular cleft takes part in the formation of the **Eustachian tube.** The dorsal entoderm of the third cleft, and to a lesser extent of the fourth cleft, gives rise to proliferations that constitute the rudiments of the **thymus gland.** On the second day a small cell thickening appears on the floor of the fore-gut between the bases of the second gill pouches. Later it bulges downwards and then becomes cut off as a closed vesicle. By the seventh day it has divided into two, and finally these give rise to the **thyroid** gland of the adult.

In the region just behind the fourth visceral pouch the gut narrows down to form the œsophagus, and on its floor in the transition region a shallow groove makes its appearance on the second day. This structure is well marked by the end of the third day, and its hinder end has grown downwards and broadened considerably. The groove is known as the **laryngeo-tracheal groove,** since it gives rise to both the larynx and the trachea, while the wider posterior portion bifurcates and develops into the paired lungs.

The œsophagus is only a short tube, and behind it the gut enlarges slightly in the third day, indicating the future position of the stomach, and then narrows down again to form the duodenal region. The liver appears at the close of the second day as two outgrowths just in front of the anterior intestinal portal on the ventral wall of the gut, *i.e.* in close proximity to the ductus venosus and the ductus Cuvieri. The anterior one, slightly the earlier to appear, grows round these vessels upwards and to the left, while the posterior one grows upwards and to the right. In the third and fourth days they

anastomose and branch freely, giving rise to a network of liver tissue around the venous trunks. With the further growth of this glandular structure its branches penetrate the ductus venosus, pushing its wall in front of them, and finally they cut it up into a canalisation of small vessels superficially resembling capillaries, but termed **sinusoids,** to indicate their different origin. These are retained as the venous vessels of the adult liver, and so the ductus pours its blood into them instead of directly into the sinus venosus, and forms the foundation of the definitive hepatic portal system.

The pancreas arises a little later than the liver, and by three diverticula. The dorsal outgrowth appears on the dorsal gut wall about opposite the posterior liver diverticulum during the third day. The two ventral rudiments appear behind the latter, and soon after the dorsal one. In a short time the three separate pancreatic growths fuse to form a common mass.

Later History of the Mesoderm.

The formation of the mesoderm and its differentiation into somites, intermediate cell mass and lateral plate have already been treated, but certain points in connection with their later history call for brief notice. By the fourth day 42 somites have been laid down, and after that 10 more are formed, but disappear later. The somites are distributed in the following manner : 1–4 enter into the skull ; 5–16 between the skull and fore limb ; 17–19 fore limb ; 20–25 between fore and hind limb ; 26–32 hind limb ; 33–35 cloacal region ; and 36–42 caudal region. The transitory somites are situated behind the last of these, and their disappearance suggests that an ancestral form possessed a longer tail.

At an early stage in each somite, as we have seen, an epithelial and a more solid portion can be recognised, but later we find that three parts become differentiated, viz. the dermatome, the myotome, and the sclerotome. The original dorsal epithelial part becomes more distinct, and its lateral region becomes fairly sharply delimited from the remainder as the **cutis plate** or **dermatome.** The mesial dorsal portion also becomes marked out as the **muscle plate** or **myotome.** This becomes thin and turns in under the cutis plate. It grows outwards, and finally reaches and fuses with the free lateral edge of the cutis plate, so that the two form a double-layered plate, sometimes referred to as the **dermo-myotome.** With the ingrowng of the lateral limiting sulcus this plate becomes disposed practically vertically. Its outer layer, the cutis plate, is gradually transformed into the dermis of the adult, and as it does so it becomes more and more closely attached to the ectoderm, which provides the epidermis.

The cells of the muscle plate elongate to form characteristic "myo-

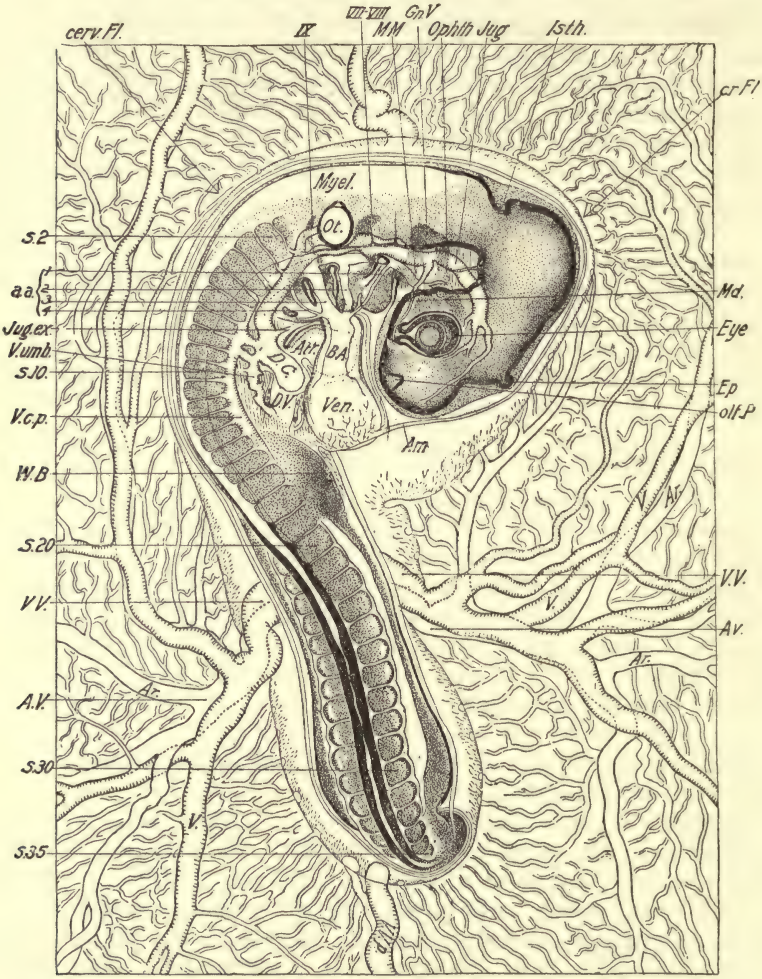


FIG. 148.—Chick embryo with thirty-five pairs of somites (72 hours).—From Lillie.

a.a., 1,2,3,4, first, second, third, and fourth aortic arches; Ar., artery; A.V., vitelline artery; cerv. Fl., cervical flexure; cr.Fl., cranial flexure; D.C., duct of Cuvier; D.V., ductus venosus; Ep., epiphysis; Gn.V., ganglion of trigeminus; Isth., isthmus; Jug.ex., external jugular vein; Md., mandibular arch; M.M., maxillo-mandibular branch of the trigeminus; olf.P., olfactory pit; Ophth., ophthalmic branch of the trigeminus; Ot., otocyst; V., vein; W.B., wing bud; V.c.p., posterior cardinal vein; V.umb., umbilical vein; V.V., vitelline vein; V.V.p., posterior vitelline vein.

blasts," that give rise later to the muscles. They are responsible for the whole of the voluntary musculature of the adult, while the

involuntary muscles are derived from the splanchnic mesoderm. To return now to the more ventral mass of the somite, we find that its cells proliferate actively and take up a position near the notochord, and it is then distinguished as the **sclerotome.** This spreads around the notochord, the neural canal and the dorsal aorta, and its cells secrete an intercellular substance. Some time afterwards the sclerotomes acquire a secondary segmentation, and each becomes divided transversely in the middle of the somite. The posterior half of each one unites with the anterior half of the next succeeding, and the blocks of tissue formed in this way of course come to alternate with the original somites. The sclerotome tissue gives rise to the skeletal elements of the axial skeleton save for a large part of the skull.

The intermediate cell mass is also termed the **nephrotome,** in order to indicate its close relation with the excretory system, and in it are developed the constituents of the kidneys. In all higher Vertebrata three successive excretory organs make their appearance, and are known as the pro-, meso- and meta- nephros respectively.

The first of these, the **pronephros,** is never functional in the chick at any time, and is represented only by degenerate remnants. Its vestigial tubules may appear in the fifth to the sixteenth somites, but are only marked in the last six or so, and there is a certain amount of variation in their number and arrangement. The first show in this region in the middle of the second day in the form of small solid cellular buds on the postero-dorsal surface of the nephrotome. These buds elongate, and their distal extremities bend over and unite with the corresponding portion of tubules behind, so that they come to form a continuous rod of cells, which represents the **Wolffian duct.** Although we term these structures the tubules, it is somewhat of a misnomer, for they are never hollow, and in the same way too the duct is solid when it is laid down, but a hollow appears towards the front end during the second day. Its posterior end grows back above the nephrotomes quite independently without contributions from the posterior members of the series, until at 2½ days it reaches and fuses with the cloaca. The lumen also spreads slowly down it and reaches the end about the third day. This Wolffian duct then is composed of two parts ; anteriorly it is a fusion of portions of separate tubules, and posteriorly it is a continuous structure. The only indication of a cavity in the tubules themselves is to be found at their lower end, where a few of them contain short hollows continuous with the cœlom, and this hollow is taken to represent the vestigial nephrotome. Furthermore, no indications of a Malpighian body are to be found in any of them. Just after the appearance of the tubule bud, the cells of the

nephrotome adjoining the somite become converted into a scattered mesenchyme, and so connection with the somite is lost. By the fourth day the pronephric tubules have disappeared.

The second kidney or **mesonephros** develops in the segments from the thirteenth or fourteenth back to the thirtieth, and some of them therefore overlap the pronephros. However, it is only those in segments 20–30 that develop typically, and these do not begin to appear until the fourth day. In this region the nephrotomes separate from the somitesand form a continuous band

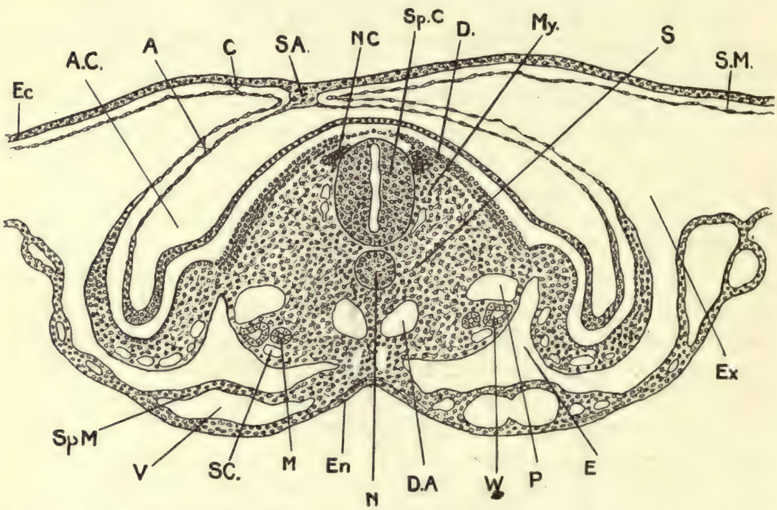


FIG. 149.—Chick embryo. Transverse section of embryo with thirty-five pairs of somites (about 72 hours).

A., amnion; A.C., amniotic cavity; C., chorion; D., dermatome; D.A., dorsal aorta; E., embryonic cœlom; Ec., ectoderm; En., Entoderm; Ex., exocœl; M., mesonephric tubule My., myotome; N., notochord; N.C., neural crest: beginning of spinal ganglion; P., post-cardinal vein; S., sclerotome; S.A., sero-amniotic junction; S.C., sub-cardinal vein; S.M., somatic mesoderm; Sp.C., spinal cord; Sp.M., splanchnic mesoderm; V., vitelline artery; W., Wolffian duct.

of tissue lying between the somite, the lateral mesoderm, the dorsa aorta and the Wolffian duct. Dorsal to this region at quite an early stage a venous trunk, the **posterior cardinal vein,** is laid down. Each tubule first appears on the ventral side of the nephrotome as a group of cells which soon acquire a hollow, and so is vesicular from the commencement. This vesicle becomes elongated and bent, and one end acquires an opening into the Wolffian duct, while the other enlarges to form the rudiment of a Bowman's capsule. Later, secondary capsules to the number of four or five arise in each somite, and altogether they form quite a noticeable swelling on the

dorsal cœlomic wall. This is the **mesonephros** or **Wolffian body,** which is the first functional kidney of the embryo.

The permanent kidney of the adult, the third to develop, is the **metanephros,** and its mode of origin is slightly different from that of the two preceding. Towards the end of the fourth day a sac-like outgrowth starts from the Wolffian duct near its point of entry into the cloaca. This grows forward as a tubular structure on the inner side of the posterior cardinal vein and above the mesonephros. The tube itself is the ureter, and it gives rise to a series of complexly branched outgrowths, the future collecting tubules. The actual secretory tubules are derived from the nephrotome tissue of somites 33–35, which accompanies the ureter as it grows forward. The metanephros has therefore a twofold origin.

Nervous System.

The early development of the nervous system has already been treated and its development outlined up to the stage when, after the closure of the neural folds, the three primary divisions of the brain had been marked out and eleven neuromeres indicated. Certain points in the subsequent differentiation of the brain call for notice.

At quite an early stage an outgrowth appears on each ventrolateral aspect of the anterior end of the prosencephalon, and it is termed the **primary optic vesicle,** to mark the fact that it is the forerunner of the eye. Across the floor of the brain, between the two vesicles, is a depression, the **optic recess.** The region in the middle line passing forwards from this to the final point of closure of the neuropore is the **lamina terminalis,** and although it is morphologically the anterior end of the brain, as a result of the flexures it becomes turned in a posterior and, finally, even a postero-dorsal direction. While at first the vesicles are in wide-open communication with the cavity of the prosencephalon, their proximal ends become closed in dorsally until they are reduced to two narrow tubes, the **optic stalks,** with small apertures, one on each side of the optic recess ; the future development of these will be considered separately later. The first neuromere swells out markedly, and at 40 hours has produced on the dorsal side a slight indentation between it and the next neuromere. This is the **velum transversum,** and a line from it to the optic recess marks the posterior limit of the telencephalon, which is therefore constituted by the first neuromere. Near the end of the second day a pair of dorso-lateral outgrowths push out from the **telencephalon.** These are the beginnings of the **cerebral hemispheres,** and they expand rapidly dorsally, anteriorly and posteriorly. They are hollow, and their cavities, the **lateral** or **first** and **second ventricles,** are in open communication with the cavity of

the prosencephalon, which is therefore designated the **third ventricle,** by wide apertures, the **foramina of Munro.** At first the wall of the ventricle thickens slowly and fairly evenly, but soon the latero-ventral region increases enormously to form the **basal ganglia** or **corpora striata,** which almost obliterate the lateral ventricles.

The next two neuromeres merge to give rise to the **thalamencephalon,** whose dorsal limits are the velum transversum in front and a broad depression behind. On the ventral side the front end is marked by the optic recess and posteriorly by an elevation in the floor of the brain, the **tuberculum posterius.** Its cavity contributes to the formation of the third ventricle. Just behind the optic recess its floor thickens to form the **optic chiasma,** and then behind this again sends down a median diverticulum, the **infundibulum.** During later development its walls thicken greatly to form the **optic thalami,** whose enlargement reduces the ventricle to a narrow vertical cleft. The roof remains thin, and in the region of the velum transversum, together with the adjacent roof of the telencephalon, it becomes modified to form the choroid plexus of the third and later also of the lateral ventricles. During the third day a small tubular median outgrowth arises from the hinder end of the thalamencephalon in the mid-dorsal line. This is the **epiphysis cerebri,** which in the chick, as in the rabbit, only develops into a glandular structure. The hinder limit of this part of the brain is definitely laid down somewhat later by the appearance of a transverse thickening, the posterior commissure.

The mid-brain or **mesencephalon** comprises two neuromeres, *i.e.* the fourth and fifth, and it comes to occupy the most anterior position in the embryo topographically, indeed, it is largely owing to the great growth of its roof that the cranial flexure is brought about. Its anterior limits have already been noted, and posteriorly it is marked off from the hind-brain dorsally by a constriction, the **isthmus,** while ventrally its limits are ill-defined. At the end of the third day little specialisation has taken place in it, and it is not until later that outgrowths from its thickened dorsal region form the **optic lobes,** and its ventro-lateral walls thicken to form the **crura cerebri.** These various thickenings of the wall lead to the reduction of the originally large cavity to a narrow lumen, the **iter.**

The whole of the cavities of the neuromeres constituting the hind-brain remain in wide open communication, and form one indivisible fourth ventricle. Its walls, on the other hand, differentiate into the **metencephalon** and the **myelencephalon.** The metencephalon includes only one neuromere, and its dorsal limit can be distinguished on the third day by the fact that it forms the hinder almost vertical wall of the isthmus, and is much thicker than the corresponding

part of the succeeding neuromeres. Its walls thicken slowly and

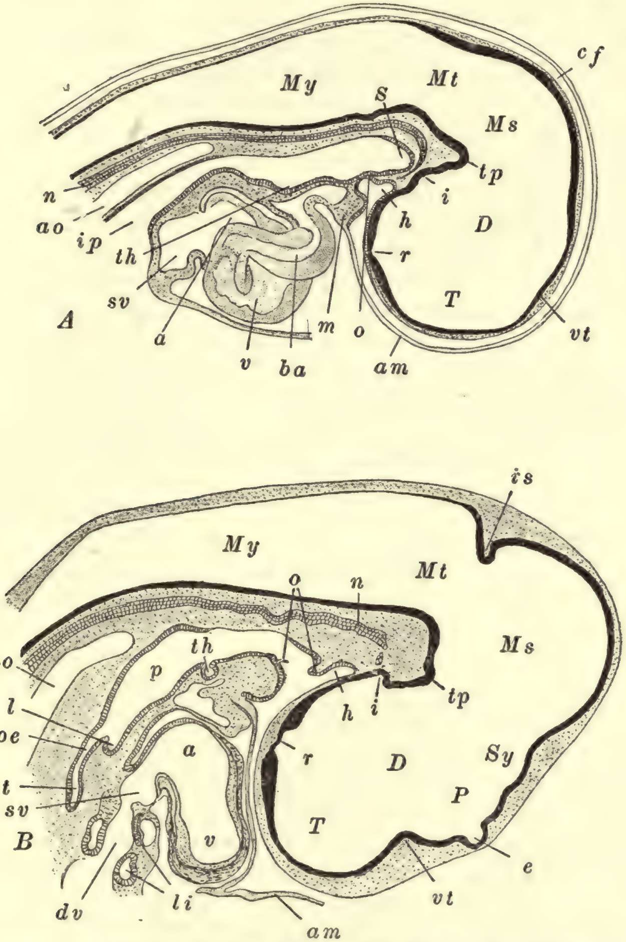


FIG. 150.—Sagittal sections through the head of the chick. In A the heart is shown in optical section.—From Kellicott.

A, of an embryo with twenty-two or -three pairs of somites (about forty-four hours); B, of an embryo with thirty-nine pairs of somites (end of the fourth day). *a.*, auricle; *am.*, amnion; *ao.*, dorsal aorta; *ba.*, bulbus arteriosus; *cf.*, cranial flexure; *D.*, diencephalon; *dv.*, ductus venosus; *e.*, epiphysis; *h.*, hypophysis; *i.*, infundibulum; *ip.*, anterior intestinal portal; *is.*, isthmus; *l.*, rudiment of lung; *li.*, liver; *m.*, mandibular arch; *Ms.*, mesencephalon; *Mt.*, metencephalon *My.*, myelencephalon; *n.*, notochord (degenerating); *o.*, oral membrane (oral plate); *oe.*, œsophagus; *p.*, pharynx; *P.*, parencephalon; *r.*, optic recess; *S.*, Seessel's pocket (preoral gut); *st.*, stomach; *sv.*, sinus venosus; *Sy.*, synencephalon; *T.*, telencephalon; *th.*, rudiment of thyroid body; *tp.*, tuberculum posterius; *v.*, ventricle; *vt.*, velum transversum.

steadily, and finally its roof becomes transformed into the **cerebellum** and its floor into the **pons Varolii.**

The posterior division of the brain is the myelencephalon. It includes the seventh to the eleventh neuromeres, and its roof remains very thin, non-nervous, and is finally transformed into the choroid plexus of the fourth ventricle. Its walls and floor thicken enormously later on to constitute the **medulla oblongata.**

Behind the hind-brain the neural canal continues backwards and shows practically no signs of segmentation. Even from the first its sides are thicker than its roof and floor, so that the lumen is elongated in the dorso-ventral direction. During the first three days of incubation the walls increase slightly in thickness, but the chief development is to be found in the cells composing them, which have differentiated into two varieties: **epithelial cells** lining the tube and stretching to its outer limits, and more rounded **germinal cells** occupying the interstices between them. From the former come the epithelial cells forming the lining of the central canal, and known as the **ependyma.** The germinal cells, on the other hand, provide the actual nerve cells constituting the grey matter of the spinal cord, and these neuroblasts, as they are termed, develop into typical ganglion cells.

Sense Organs.

The three main organs of special senses, taking them in the order in which they appear, are the eye, the ear and the olfactory organs.

Eye.

Early in the second day, before the neural folds have met, the lower side walls of the fore-brain region show distinct outbulgings. These are more marked upon the closure of the folds, and, as has been noted above, the aperture between them and the fore-brain cavity becomes considerably constricted, forming at last a tubular **optic stalk.** The distal portion is dilated to form the primary optic vesicle, and its outer wall almost touches the ectoderm, which commences to thicken in this region at quite an early stage, giving rise to the lens rudiment. The outer and ventral wall of the vesicle also thickens and sinks inwards towards the inner wall. Simultaneously with this invagination process the rudiment of the lens also sinks in to form a thick-walled depression that at first almost fills the inside of the cavity on the outside of the optic vesicle. The invagination continues until the thicker originally outer wall comes to lie close against the thinner original mesial wall, and so the cavity of the vesicle is obliterated. In this way a double-walled **optic cup** or **secondary optic vesicle** is formed, whose cavity represents the **posterior** or **vitreous chamber** of the eye. At the same time the lens invagination gets deeper, becoming transformed into a relatively

large pit. The edges of this come together, and finally it becomes cut off from the superficial ectoderm as a thick-walled spherical vesicle, that almost fills the opening of the optic cup by about the end of the third day. The inside thickened layer of the optic cup is the beginning of the sensitive layer of the retina, while the outside part is the pigment layer, and pigment is formed in it during the fourth day.

It has been noted that not only is the original outer wall of the primary vesicle involved in the invagination, but also the ventral wall back to the optic stalk. Thus it comes about that when the optic cup is first formed it is incomplete on the ventral side. The adjacent regions expand and fill in this gap to a certain extent, but

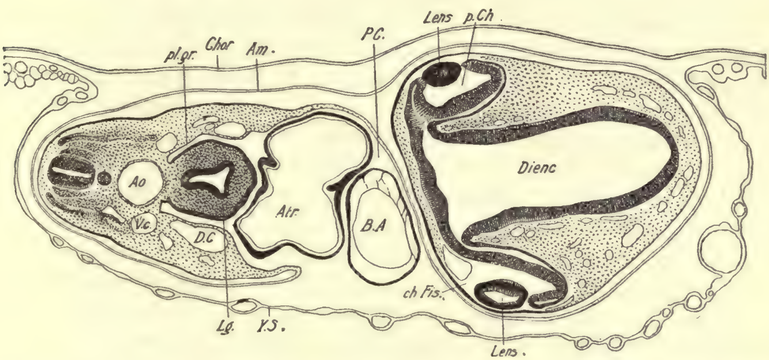


FIG. 151.—Transverse section through the eyes and heart of an embryo of about thirty-five pairs of somites.—From Lillie.

ch.Fis., choroid fissure ; D.C., duct of Cuvier ; Lg., lung ; pl.gr., pleural groove ; V.c., posterior cardinal vein ; Y.S., yolk-sac ; Ao., aorta ; Chor., chorion ; Atr., atrium ; Dienc., diencephalon ; p.C., parietal cavity ; p. Ch., posterior chamber of the eye ; am., amnion ; B.A., bulbus arteriosus.

for quite a while a narrow cleft, termed the **choroid fissure,** is left running from the rim of the cup back to the optic stalk. The presence of this fissure is of considerable importance to the future course of development of the eye. In the first place it leaves the whole of the inside layer of the retina in communication with the stalk, and so when the nerve cells of the inside of this layer send out their axons these can grow back along the stalk as the **optic tract** into the brain. This leads to the disappearance of the cavity of the stalk, and its transformation into the definitive optic nerve. Secondly, the fissure allows that part of the adjacent mesoderm from which the vitreous humour will be derived to spread into the optic cup, and it also allows for the ingrowth of the retinal arteries and veins.

At a later stage the lens withdraws from the ectoderm, leaving a space representing the anterior or aqueous chamber. The superficial ectoderm becomes thinner and transparent, forming the **conjunctiva.** Thus it will be seen that the parts of the eye essential to vision, *i.e.* the conjunctiva, the lens, the retina and the optic nerve, are derived directly from the ectoderm as in the case of the first two, or indirectly from it, via the brain in the case of the second two. All the remaining or accessory parts are derived from the mesoderm.

Ear.

At thirty hours, or soon after, a thickened patch of ectoderm appears on each side of the hind-brain, just in front of the first pair of somites and nearly above the hyoid arch. These are the **auditory plates,** the rudiments of the membranous labyrinths. These plates increase in size and sink in the middle to form the **auditory pits,** whose edges approximate until by the third day we find a large **auditory sac,** formed and connected with the surface by a narrow tubular canal. This canal is the **endolymphatic duct,** homologous with the similarly named structure in the dogfish. At the end of the third day it loses its connection with the exterior, and so the auditory sac comes to lie freely in the head mesenchyme. Some days later the distal end of the ductus enlarges to form an **endolymphatic sac,** that finally extends along the mesoderm above the dorsal-lateral surface of the myelencephalon. The auditory sac elongates dorsoventrally, and soon an internal ridge appears, marking its division into a dorsal portion, the **utriculus,** and a ventral region, the **sacculus.** At first the end of the duct opens into the upper corner of the utriculus, but this part subsequently expands dorsally on the outer side of the ductus, which thus comes to open into the inner side of the utriculus.

About the fifth day three narrow grooves appear in the superior chamber in the relative positions of the semicircular canals. They grow out as thin hollow expansions, their inner margins fuse save at two ends, thus converting them into tubular canals opening at each end into the utriculus. Gradually they move outwards, carrying along the line of fusion of their edges a thin sheet of the sac wall with them, but with the breaking down of this sheet and the enlargement of one end of each to form an ampulla they become transformed into typical semicircular canals. The sacculus gives rise to an outgrowth that later develops into the cochlea. At first the walls of the auditory sac are moderately thick, but with its enlargement they become much thinner save in certain areas, which mark the positions of the **maculæ, cristæ** and **papillæ** of the adult ear.

The essential part of the ear then, like the eye, is derived from the ectoderm.

From the mesenchyme surrounding the auditory sac are developed, first, a membranous covering for the labyrinth, with which it becomes closely associated; secondly, a loose tissue that becomes converted into **perilymph,** and outside this a denser layer, in which the cartilage and afterwards the bone is laid down.

The hyomandibular pouch arises in two portions: a large ventral part similar to the remaining gill pouches, and a smaller dorsal portion which is perforated only for a short time. The ventral portion is transitory, while the dorsal piece is persistent throughout life as a part of the tympanic cavity. The remaining portion of the cavity and the Eustachian tube are differentiated from the dorsal wall of the pharynx in this region. The **external auditory meatus** arises as an ectodermal ingrowth from the surface of the head in a region that was originally between the dorsal and ventral portions of the hyomandibular pouch.

Olfactory Organ.

The olfactory organs take their origin in much the same way as the ear, as a pair of thickened patches of ectoderm, the **olfactory plates,** lying on the side of the head in the fore-brain region in front of the eye. They appear towards the close of the second day. The plate invaginates and forms a fairly deep **olfactory pit** with a wide opening, which, owing to a more rapid growth of the dorsal region of the head, comes to lie on the antero-ventral side of the head. The openings of the two pits are separated in the middle line by a broad band of tissue, the **fronto-nasal process,** which thus forms their inner margins as well as the anterior boundary of the primitive mouth. The lateral wall of the aperture is elevated during the fourth day to form the **external nasal process.** In the fifth day this external process becomes linked with fronto-nasal process by a bridge of tissue that separates the olfactory opening into parts, one above it and one below. The bridge itself is a rudiment of part of the upper jaw, and consequently as it enlarges the two apertures become more and more widely separated; the upper one moving dorsally to form the **external naris,** and the lower one, lying in the stomodœal area, passes into the buccal cavity to become the **internal naris.**

Lepus.

In the previous chapter, when considering the development of the mammal, only the changes in the embryo itself were taken into account, and it was indicated that while these were in progress others

more external and extra-embryonic were going on. These lead to the formation of the characteristic membranes enclosing the embryo and its attachment to the uterine wall, and we must now consider them. The membranes are on the whole closely similar to those in the chick in origin, but have a quite different fate. The amnion loses most of its value as a protection, the yolk sac is practically a vestigial remnant, the allantois loses most of its respiratory and excretory functions, being mainly concerned with bringing the embryo into relation with its food supply, and the chorion either wholly or in part becomes the chief organ of nutrition and excretion. There is considerable diversity in the parts played by the various structures in different groups of mammals.

By the time the ovum reaches it the mucous membrane lining the wall of the uterus has become enlarged, highly vascularised, and thrown into a series of folds, and the trophoblastic wall of the vesicle is soon brought into contact with it. In the rabbit and certain other forms it becomes attached to the wall of the main cavity of the uterus, a condition known as **central implantation.** In man and other species, however, the vesicle bores its way through the superficial layers of the mucous membrane, which closes over behind it, and so it becomes buried, a condition known as **interstitial implantation.** In the rabbit a horse-shoe-shaped area of the trophoblast, behind and lateral to the embryonic rudiment, becomes modified to form a layer of enlarged actively growing cells, termed the **trophoderm,** and this is responsible for its attachment to the mucosa. In man this change takes place over the whole surface of the vesicle.

Amnion and Chorion.

The processes resulting in the formation of the Amnion and the Chorion in the rabbit closely resemble those in the chick. The wing-like extension of the mesoderm from the axial line leads to the formation of quite a large proamniotic area. The first of the folds to appear is the tail fold, and while this is in progress the head bends down and pushes its way into the proamniotic area, whose anterior margin soon rises up into a fold. Lastly, the lateral folds appear joining the preceding ones, and they all grow upwards to fuse over the top of the embryo. The fusion is more complete than in the chick, and so only a small sero-amniotic knot is left. The separation of the walls of the folds then leads to the formation of (*a*) the amnion immediately above the embryo, and (*b*) the chorion in close contact with the trophoblast. Within the former is the amniotic cavity, and between it and the chorion is the extension of the extra-embryonic cœlom. The relations of ectoderm and mesoderm in these two folds is just as in the chick. The mesoderm later invades

the proamniotic area, and the folds pass in under the embryo until

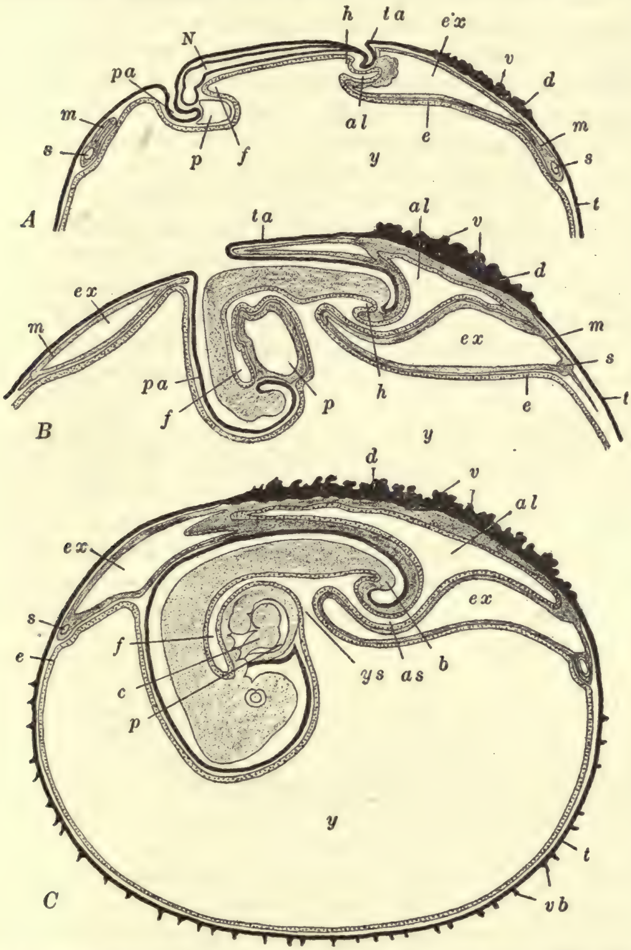


FIG. 152.—Diagrams of the formation of the embryonic membranes and appendages in the rabbit.—From Kellicott, after Van Beneden and Julin (partly after Marshall).

Sagittal sections. A, at the end of the ninth day; B, early the tenth day; C, at the end of the tenth day. Ectoderm black; endoderm dotted; mesoderm grey. *al.*, allantois; *as.*, allantoic stalk; *b.*, tail bud; *c.*, heart; *d.*, trophoderm; *e.*, entoderm; *ex.*, exocœlom; *f.*, fore-gut; *h.*, hind-gut; *m.*, mesoderm; *n.*, central nervous system; *p.*, pericardial cavity; *pa.*, proamnion; *s.*, marginal sinus (sinus terminalis); *t.*, trophoblast; *ta.*, tail-fold of amnion; *v.*, trophodermal villi; *vb.*, trophoblastic villi; *y.*, cavity of yolk sac; *ys.*, yolk stalk.

they completely surround it, save at the places where the allantoic and yolk sac stalks leave it. In the rabbit the amniotic cavity never

becomes very large, but the extra-embryonic cœlom or exocœl dilates until it practically fills the cavity of the blastodermic vesicle.

In man the formation of the amnion is not accompanied by the production of folds, but, as pointed out in the last chapter, the primitive amniotic cavity appears as a space between Rauber's layer and the embryonal shield. The manner of its formation is such that no proamnion appears. The final relations of the folds are the same in the two cases, however, in spite of their different origin. The human amniotic cavity enlarges very rapidly, and finally fills the whole of the inside of the vesicle save for the part occupied by the yolk sac and allantoic stalks, which therefore come to be, as it were, bound together to form a combined structure, the **umbilical cord.** The dilatation of the amnion is so great that it completely obliterates the exocœl, and the external mesoderm layer of the amnion comes to lie close to the inner mesoderm of the chorion and the two fuse.

In the rabbit a vascular area is established in a normal way in the splanchnopleure, and it is bounded by the sinus terminalis. The rapid extension of the exocœl, which soon reaches the sinus terminalis, limits the extension of the vascularisation to the upper side of the yolk sac. Beyond the vascular area the mesoderm never extends, so that the remaining hemisphere of the vesicle, termed the **omphalopleure,** is simply bilaminar. Thus the chorion is limited to the upper regions.

Yolk sac.

At an early stage the yolk sac in the rabbit occupies the main part of the blastodermic vesicle, and its splanchnopleuric portion is separated from the chorion by the exocœl. In this species the entoderm of the sac develops but slowly, so that for a considerable time it is incomplete on the ventral side. Finally, it is completed, and this last portion lies in contact with the chorionic ectoderm and the mesoderm but slowly pushes its way in between them. Thus it is that in this form the yolk sac is only splanchnopleuric in its upper portion, while below its entoderm is in contact with the blastodermic ectoderm. The extra-embryonic cœlom expands markedly in the rabbit, and so compresses the cavity of the yolk sac until this structure finally takes on a sort of umbrella shape. The long narrow yolk sac stalk represents the handle, and the flattened expanded sac itself the cover. The splanchnopleure becomes richly vascularised and has a well-developed sinus terminalis, and its main vessels are termed the **vitelline,** or, perhaps more frequently, the **omphalo-mesenteric** arteries and veins respectively. The veins penetrate the liver and enter the hinder portion of the

sinus venosus. In the adult their embryonic portions form the hepatic portal veins.

In man the yolk sac is very different: it is completed at a fairly early stage, and is quite small. It never reaches the far side of the blastodermic vesicle, and so appears as a small bladder suspended in the exocœl by the yolk sac stalk. It then diminishes in size, and

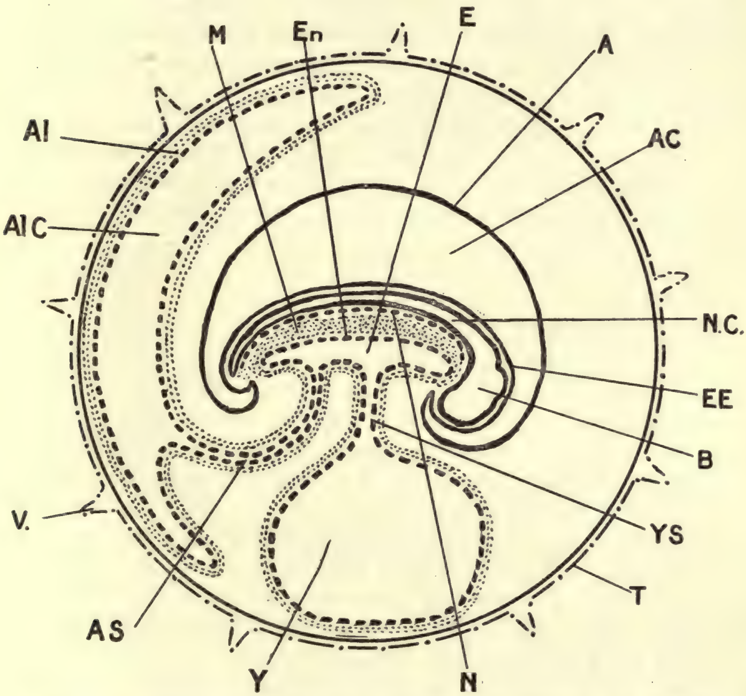


FIG. 153.—Generalised diagram of the fœtal membranes of a mammal, adapted from Hertwig.

A., amnion; A.C., amniotic cavity; Al., allantois; Al.C., allantoic cavity; Al.S., allantoic stalk; B., brain; C., chorion; E., enteron; E.E., embryonic ectoderm; En., embryonic entoderm; M., embryonic mesoderm; N., notochord; N.C., neural canal; T., trophoblast; V., villus; Y., yolk sac; Y.S., yolk sac stalk.

as the expansion of the amniotic cavity brings about the formation of the umbilical cord, the yolk sac becomes first of all reduced to a small blind cœcum and finally disappears altogether.

Allantois.

The **allantois** is also subject to considerable variation among various groups of the Mammalia, but on the whole its relations are

similar to those in the chick. Despite the differences in its fate in various forms it is always of importance, because its blood-vessels form the vascular supply of the placenta and are very similar throughout the mammalian series. The allantois appears as an outgrowth of the hind gut and expands freely in the exocœl, which it traverses and reaches the chorion in the trophodermic region. It unites with this layer to form the **allanto-chorion,** and so almost from its beginning forms a link between the embryo and the portion of the blastoderm most intimately related to the uterine mucosa. The vessels consist of a pair of **umbilical arteries** and a pair of **umbilical veins,** and through them the chorionic region, previously without vessels, becomes highly vascularised. This region is destined to form the placenta, which therefore receives its embryonic blood supply via the allantonic vessels, and it is important to remember that this is true, however small or large the actual allantois may be.

Placenta.

The term **placenta** is applied to the organ that in the Mammalia forms the connection between the lining wall of the maternal uterus and the membranes surrounding the growing embryo. From the entirely different mode of development in the chick it is obvious that this structure is not represented in it. Structurally the placenta is a complex, consisting of a very close apposition between the fœtal membranes and the uterine tissues, or more frequently and typically it is an actual and complicated interpenetration of the two that results in bringing their blood streams in close proximity to one another. Functionally it serves in the early stages to anchor the embryo to the uterine wall, and later it is the centre wherein the dissolved salts and nutrient material of the parental blood can transfuse into the fœtal blood, thus providing the materials necessary for growth. Also it provides a means whereby the excretory matters, both nitrogenous substances and carbon dioxide, can diffuse from the fœtal to the maternal blood, and so it also serves as an organ of excretion.

In the early stages of development the vascular walls of the yolk sac may play a part in these functions, and so we speak of a **yolk sac** or **omphalopleural placenta,** but sooner or later in all the higher mammals, *i.e.* the **Eutheria,** an allantoic placenta is developed, and this is one of the distinguishing characteristics of the order.

We have already considered briefly different forms of behaviour in the early implantation of the developing ovum; it may be central, or interstitial, or in certain cases it is **eccentric,** that is to say, lies in a fold of the mucosa to one side. It is obvious that this will

affect the relation of the membranes to the uterine wall, and so the type of placenta formed, but it gives no indication of the enormous variations that are to be met with in the details of the origin, formation and final constitution of this highly important structure. These are matters of considerable complexity, and outside the scope of this work, so that we can only consider the outlines of them in the case of the rabbit.

The uterine mucosa in the non-pregnant rabbit is arranged in a series of longitudinal folds, of which two, situated one on each side

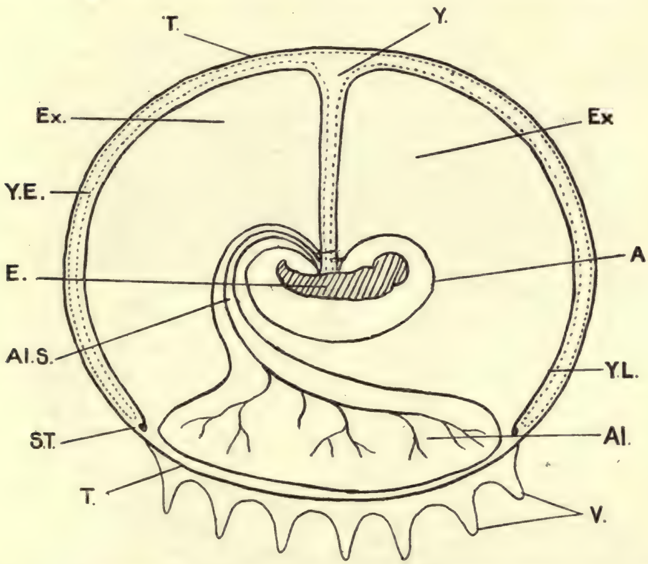


FIG. 154.—Diagram of section of fully formed blastodermic vesicle of *Lepus*, adapted from Hertwig.

A., Amnion ; Al., allantois ; Al.S., allantoic stalk ; E., embryo ; Ex., exocœl ; S.T., sinus terminalis ; T., trophoblast ; V., villi ; V.L., vasuclar layer of yolk sac ; Y., yolk sac ; Y.E., yolk sac entoderm ; Y.S., yolk sac stalk.

of the line of attachment of the broad ligament, are larger and more important than the remainder : they are termed the **placental ridges.** They are separated by a groove, and generally when the blastocyst adheres to the uterine wall it is in such a position that the embryo is near and parallel to this groove. As we have seen previously, a horse-shoe-shaped band of trophoderm is established at an early date, and this lies in the region touching the ridges. The cells of this delimited area multiply rapidly and fuse, so that they form a syncytium, which is extremely active, and in which cell walls cannot be made out. The uterus, and particularly the placental ridges,

enlarge greatly in early pregnancy, and the ridge capillaries dilate considerably. The uterine epithelium in touch with the trophoderm disintegrates and is absorbed, and the syncytium actively grows down into the underlying mucosa in the form of a series of thin plates arranged in the form of an irregular honeycomb. These grow in, absorbing the tissue of the mucosa as they do so, and come to surround a number of the maternal capillaries. Finally, even the

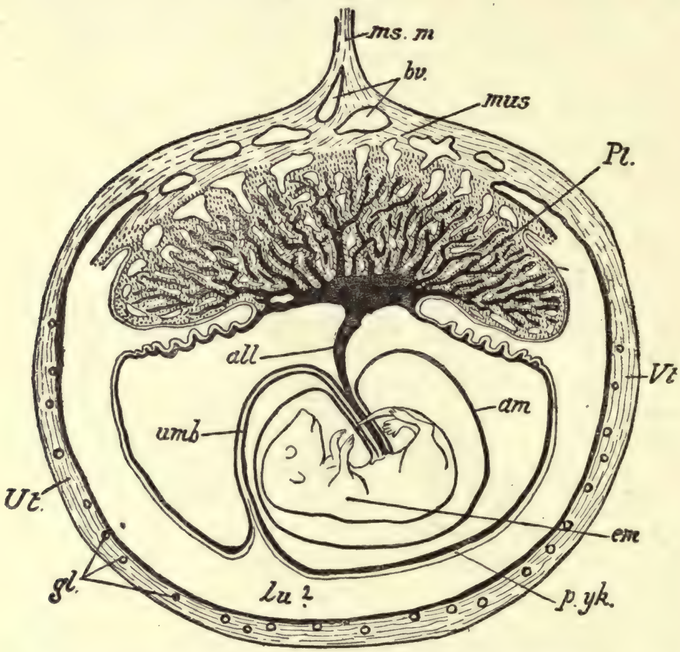


FIG. 155.—Diagrammatic transverse section of a pregnant uterus, illustrating the later phase of placentation.—From Bourne.

all., allantois ; *am.*, amnion ; *bv.*, uterine blood-vessels ; *em.*, embryo ; *gl.*, uterine glands *lu*², secondary lumen of uterus ; *ms.m.*, mesometrium ; *mus.*, muscular wall of uterus ; *Pl.*, allantoidean placenta ; *p.yk.*, proximal wall of yolk sac ; umb., stalk of yolk sac ; *Ut.*, uterus.

walls of the capillaries break down, and so the parental blood comes to circulate in a series of sinus-like spaces in the trophoderm.

While this has been going on the allantois has grown out and fused with the chorion, bringing with it its mesoderm in the form of a richly vascularised mesenchyme. This mesenchyme grows downwards between the trophoblastic lamellæ, and so forms a series of long papillæ, known as **villi.** Thus we have a series of tongues of mesenchyme containing embryonal blood-vessels and surrounded by the trophoblastic tissue, in whose sinuses circulates the maternal blood.

This is the essential arrangement of the adult placenta, but it is somewhat masked by the facts that in the first place the embryonic capillaries enlarge considerably, and in the second the trophoblastic tissue and allantoic mesenchyme thin out until they become almost negligible. So it is that the embryonic capillaries are practically bathed in maternal blood, and an interchange of substances between the two blood streams is simply a question of diffusion. It is important to notice, however, that in spite of their proximity the two blood streams never actually intermingle, owing to the fact that the embryonal capillaries always retain intact their endothelial walls.

We see then that the placenta when fully formed is a very intimate union between fœtal membranes and uterine mucosa. It has the form of a flattened, disc-shaped (hence the term placenta=a flat cake), spongy, vascular thickening composed of two lobes, one related to each original placental ridge. The embryo is attached to this by means of the allantoic stalk carrying the blood-vessels, and around which the yolk sac stalk becomes slightly twisted to form a common umbilical cord. From its shape this type of placenta is termed discoidal, and it is somewhat similar but not bilobed in man. Owing to the fact that the fusion is so complete, a superficial part of the uterine mucosa, mainly blood, comes away from the deeper layers with the allantoic portion at birth, and so the placenta is spoken of as **deciduate.** At parturition the amnion and chorion rupture and the embryo is born attached to the placenta and remains of the membranes by the umbilical stalk, which is gnawed through by the parent. The biting squeezes together the blood-vessels and the small remnant soon shrivels up, leaving only an almost indistinguishable umbilical scar or **navel**, which marks the point where the animal when an embryo was attached to the placenta.

We have seen then that as the mammal has descended from an ancestor laying a large heavily yolked telolecithal egg, it is provided with a series of membranes on the whole very similar to those of the chick and homologous with them. Their original functions in relation to the absorption of the yolk and protection of the embryo disappear, and they take on entirely different ones, still to a certain extent protective, but in the main concerned with excretion and nutrition.

CHAPTER XVII

EVOLUTION, VARIATION AND HEREDITY

The study of Biology is usually divided for convenience into Botany and Zoology, and so far we have been concerned in the main with the investigation of the facts of these subjects, particularly as they relate to animals. The scientist is naturally concerned with facts, for these of themselves are of great importance and often, as in the study of medicine, of practical utility in conducting the affairs of life. But while in the early stages it is necessary to devote considerable time to acquiring a knowledge of these facts, and the methods by which they can be verified and fresh ones discovered, sooner or later one inevitably tries to put them in some sort of order, to relate them to one another and generally to try and find the causes that are working to produce them. This leads us into a field of work where theories and facts are intermixed, often to such an extent that it is impossible to draw a distinction between them. When we pass on to examine certain of these theoretical points the separation of Botany and Zoology, that is, the treatment of plants and animals as beings that can be placed in isolated compartments, is no longer convenient or possible. We may indeed draw our illustrations mainly from one or other kingdom, but they are only examples and as a rule serve to illustrate principles that apply directly or with only slight modification to both. Sometimes we are able to see as the result of a number of observations that certain definite conditions, which we term the cause or causes, are inevitably followed by the appearance of definite phenomena which we call the effect. When we can express this relationship in such a general way that it includes a number of different phenomena, we say that we have formulated a natural "law." It will be seen, however, that the word "law" has a different meaning from that intended when used in ordinary conversation. There is no implication that there is a code of regulations drawn up, the breach of which is followed by punishment, but simply that a certain effect is always produced as the result of certain previous conditions.

The most fundamental of the theories to be considered are those that concern Evolution, or better, Organic Evolution. This idea of

successive change or evolution has come to be one of the most widespread generalisations of modern times and is not limited to the sciences in which it was first propounded, but has now been applied to practically every branch of human thought. We can recognise clearly three distinct sorts of evolution: (1) Inorganic evolution, that is, the formation of the world and the inorganic materials in it; (2) Organic evolution, that is, the production of the many and varied forms of living beings that fill the world to-day; and (3) the evolution of things with which man has dealt, such as the growth of languages, religions and human institutions, the development of art, of buildings, of machinery and so on. It is with the second of these, namely, **Organic Evolution,** that we are practically entirely concerned.

Two very different things must be clearly borne in mind from the outset: one is that the occurrence of organic evolution is now generally accepted as a fact by all who study even a little biology; and the other is that there is probably no explanation of it as a process, of the exact causes at work, and the precise manner in which they operate has been generally admitted to be satisfactory. The two things, however, that is, evolution itself and the theories to explain it, must be kept quite distinct, and the failure to do so has led to much confusion of thought, particularly in semi-popular writings, but also in some scientific works. Thus it is by no means uncommon to find in poorly informed quarters a statement to the effect that, in view of the criticisms that have been levelled at Darwin's *theory* of evolution, evolution itself is no longer believed in by them. Nothing could be further from the truth, for the *fact* of evolution remains unchallenged and it is only the explanation of the causes at work that is questioned.

It is desirable, in order to appreciate the more modern views on evolution and some of the theories that have been put to explain it, to examine quite briefly the opinions that were previously held and so approach our present conceptions on the subject from the historical standpoint.

From the time of the Greeks, who had a very good knowledge of Biology and indeed made some attempts to explain the origin of the diversity of living things, up to the beginning of the eighteenth century, Biological Science was in a chaotic state and in the first part of that period, instead of advancing, fell back. Throughout the Middle Ages little thought was given to the subject, and it was a matter of general belief that there had been a special act of creation and all the animals and plants we now see were created exactly as they are at present. Each particular type was considered fixed and unalterable and spoken of as a **species.** When fossil remains of

animals long since extinct were found, they naturally presented some difficulty and were regarded by some as misfits, animals of which models had been made and then rejected, others saw in these fossils traps laid by the evil one for the undoing of the faithful.

In the revival of natural sciences in the eighteenth century, Biology became once more a subject of study in which many valuable observations were made, and it soon became evident that enquiring minds demanded some satisfactory explanation of the enormous variety of living beings inhabiting the earth.

To enable biologists to deal with the mass of observations that had gradually accumulated and was fast being added to, it early became necessary for them to be reduced to some sort of order which in the first place meant a satisfactory system of classification. The English naturalist, John Ray (1627–1705), was the first to really attempt a classification of living things on the basis of anatomical resemblance. He framed a definition of a species to be used as a unit, and upon this, subsequent classifications were based. Another noteworthy contribution that he made was the separation of flowering plants into Monocotyledons and Dicotyledons, and he also called attention to the important fact that it was impossible to rely entirely upon one organ in a group of organisms in any system of classification.

Karl Linné or Linnæus (1741–1789), a Swede, rendered the growing biological science a great service by devising a system of naming animals and plants. To each he gave two names, the first or generic name designating the genus or group of similar types to which it belonged, and the second or specific name designating the species or collection of almost identical forms among which it could be included. He himself held, "There are as many different species as there were different forms created in the beginning by the Supreme Being." The species was thus considered as established once and for all without the possibility of being changed. He did a great amount of important work, naming and describing a large number of animals and plants and arranging them in groups, and many of his names are retained to-day. In consequence of this his name had considerable authority, and his idea of the fixity of species was widely accepted.

Cuvier (1769–1832) carried the Linnæan system a step further, by grouping genera together in larger categories united by a common basis of structural similarity, and in this way laid the foundations of the science of Comparative Anatomy. Further, he was the first biologist to study fossil forms, and more noteworthy still, he discovered the striking palæontological fact that the lower and consequently more remote the layer from which fossils are obtained the

less the fossil species resembled modern ones. This fact he was unable to interpret correctly, owing to his belief in the immutability of species, and he held the disappearance of the fossil forms to be the result of sudden cataclysms, such as earthquakes or floods, which annihilated successive faunæ or sets of animals living on the earth.

Another French naturalist, Buffon (1708–1788), opposed this view of sudden geological changes, and maintained that these fossil remains were the result of topographical changes in the configuration of land and water and to climatic changes, leading to the extinction of certain forms of life.

Several thinkers, notably Goethe, 1790, Oken and Erasmus Darwin, 1794 suggested the possibility of change or transmutation. Goethe held that the various organs of a plant were modifications of the one organ the leaf. Darwin called attention to the similarity between the arm of man and the wing of a bird, and claimed that this indicated a relationship between the two. Apart from these men the generally accepted opinion was that species were unalterable.

The first serious attempt to grapple with the problem was made by Lamarck (1744–1829), in his "Philosophie Zoologique," in 1809, a little more than a century ago. In this book we see recognised for the first time the fact that animals are not just isolated beings, but bear some relationship one to another, and also that they can be arranged in a series from the most primitive to the highest form. His series is not the one we now recognise, but it *was* a series, and indicated an evolution which the author not only recognised but tried to account for. At the same time he saw that vestigial structures and remarkably well-developed organs needed some sort of explanation. He held that new forms were made in the past and are still being made by the modification of pre-existing species. The modifications were due to the surroundings in which the animal lived and its attempts to suit its life to them. Thus it was suggested that the giraffe got its long neck by constantly trying to feed on leaves higher and higher up the trees; wading birds have long legs because they wished to go into the water after their food but at the same time avoid wetting their feathers. Conversely the mole's eyes are very small because it no longer uses them, the teeth of the whale disappear as it swallows its food without mastication, and so on.

These views were based on the well-known fact that during the life of an individual those organs that are used increase in size, *e.g.* the arm of a blacksmith, and those that are not used decrease. The actual alteration in the individual would be small but it would be transmitted to the offspring, and when continued generation after generation the effect would be cumulative. The particular view is termed "*use inheritance*," or, since the character is acquired during

the lifetime of the individual and handed on to the young, "*the inheritance of acquired characters*," a point to which we shall return later. No satisfactory evidence has been obtained to show that such inheritance occurs at any rate in the crude form in which it has just been stated, and this doctrine and all it implies, usually spoken of as *Lamarckism*, is not generally held to-day. It shows a clear recognition of certain important underlying principles however. The first is the idea of modification or mutation of species, the second is the fact that structural characteristics are handed on from parent to offspring, and thirdly that animals are on the whole well suited for the life they lead.

Here we meet for the first time with a definite recognition of and expression of the idea of Organic Evolution, which has since been much extended, and in its modern form states that the various members of the animal and vegetable kingdoms, as we know them to-day, have not existed for all time, but are the result of a long continuous series of changes. These slow changes have been in progress since an early period of the earth's history, and are still going on and will continue until organisms cease to exist. They have resulted in the production of higher and higher forms of life, or, to put it in another way, the forms we see to-day have been evolved or developed from lower forms, and these from still lower ones, and so on. There has been a gradual progress from the simple to the more and more complex and specialised. This change in the case of certain domestic animals and plants is an observed and observable phenomenon even in the course of a man's lifetime. We now grow in our gardens many kinds of plants that were unknown to our forebears, and, we all know, new "varieties," as they are termed, are added year by year. Not only does this apply to flowers such as roses, etc., but to our crops like wheat, fruit and potatoes, and also to animals. Still it has been questioned in the past and is sometimes questioned to-day by people with little biological knowledge, whether such a conception of change is generally applicable to animals and plants in the state of nature. The answer is undoubtedly yes, but before going on to consider the theories which attempt to explain it, we shall do well to stop for a while and examine the evidences for the occurrence of organic evolution. These may be dealt with conveniently under four heads: Anatomical, Embryological, Geographical and Palæontological evidence.

Anatomical Evidence.

We have had in this course many concrete examples of facts relating to evolution, so that it is only necessary to call attention to the general plan of the evidence. We find that animals, and

plants too for that matter, are not simply isolated forms unrelated to one another, but can be arranged in groups, showing marked similarity among themselves. The members of the smaller groups, the genera, are very closely related and often differ mainly in size, proportion of parts, and colour. Consider, for example, the cat family, the *Felidæ,* we have *Felis leo* the lion, *F. tigris* the tiger, *F. pardus* the leopard, *F. lynx* the lynx, *F. concolor* the puma, *F. domesticus* the domestic cat, and other less known species. Every one is sufficiently familiar with the appearance of all these to recognise that the differences between them are mainly those of size, colour, markings, and proportion of parts. They are, however, all obviously similar animals, and indeed in a standard text-book of mammalian anatomy we read, " The Tiger (*F. tigris*) is so closely related to the Lion that it is chiefly by external characters that the two species are distinguished." This likeness is most reasonably explained by supposing them all to be the modified descendants of one original distant ancestral " cat." Larger groups, *e.g.* Amphibia, Reptilia, Aves, and Mammalia, although differing enormously in many respects, are very obviously built on the same general plan. They have a skeleton consisting of: a vertebral column, *i.e.* a number of essentially similar bones in a series forming the main support of the body, and a canal for the reception of the spinal cord ; a skull, *i.e.* a collection of bones giving lodgment to the brain, the olfactory optic and auditory organs, and furnishing a pair of jaws ; pectoral and pelvic girdles, giving support to paired pentadactyl limbs, and so on with the other systems. All of them exhibit the same basal plan, and where differences occur we can see very often that the change enables the animal to be better suited to its environment. The most obvious explanation of this is to suppose that they have all descended from an ancestral form that exhibited the general plan in a simple unmodified condition. Similar evidence confronts us in every group, large or small, in the animal and vegetable kingdoms. Why is it that our own fore limb, the fore limbs of a cat, a whale, a bat, and a bird are all composed of essentially similar parts although adapted for quite different purposes ? The simplest answer is that they all represent modifications of one and the same thing.

We saw in *Scyllium* that the ear is composed of a complex membranous labyrinth, and lies near the first gill cleft, and is concerned largely with equilibration. In the frog, which no longer needs a gill cleft, since it is an air-breathing form, the outside of the cleft is covered by a tightly stretched membrane, the tympanum, which becomes accessory to the ear. The old ear, as in *Scyllium,* is still present though more developed, but hearing becomes a more important function, and for increased efficiency further structures, the

tympanum, columella auris, etc., are added to it. Finally, in the rabbit the process of improvement is carried still further, and we have added an external auditory meatus, a pinna, a chain of ear bones. Also to meet the much higher function of hearing we find a part of the labyrinth specialised to form the cochlea, a very complex apparatus for receiving and analysing sound vibrations. So that we can actually trace the building up of the structures of the higher animals through a successive series of stages in lower forms. The reverse is also true, for the complex branchial skeleton of *Scyllium* can be traced through the stage in *Rana* up to that in the mammal, where it has been reduced to the hyoid bone, and is utilised for a different purpose from its original one.

Yet another form of evidence is that supplied by what is known as **vestigial structures.** We all of us possess muscles for moving our ears and scalp, yet only a few are able to employ them, and even then the movements serve no useful purpose. Why should such structures be present at all? They are handed down to us from ancestors to whom they were useful. The appendix in man, the tiny limbs in certain snake-like lizards, a small spur representing a hind limb in *Boa constrictor*, the ligamentum arteriosum, and a multitude of other structures are to be similarly explained.

Embryological Evidence.

In the portions dealing with embryology another variety of evidence has been brought out. Thus, for example, we find that the bird and the mammal pass through a stage of development in which the heart, the blood-vessels, and the pharyngeal region are in a condition resembling that found permanently in the adult fish, so that the whole type of circulation is the same and adapted to the aeration of the blood in the gills. Attention was first called to facts of this sort in "Vestiges of the Natural History of Creation," a book published in 1844 by Robert Chambers, which appeared anonymously, since the author feared it would damage his business. Observation of a large number of instances similar to this soon led to the formulation of what has been termed the **Recapitulation Theory,** or the Fundamental Law of **Biogenesis.** According to this law, the reason for the appearance in the embryo of conditions or structures that obtain permanently in the lower groups is that each animal in its development recapitulates, or at any rate hints at, the past development of the race. This has been expressed in the aphorism, Ontogeny (the history of the individual) reproduces Phylogeny (the history of the race).

It is unnecessary to labour the point, however, that the record of the race history kept in the developmental stages of any animal is

modified, blurred and incomplete. For while there is a circulatory system in the chick similar to that in a water-dwelling fish, yet the embryo chick is not a fish, and could not utilise this arrangement for aquatic respiration. The history is often enormously modified to suit the actual requirements of the young animal, and so on.

Striking applications of this law are to be met with in certain groups of the animal kingdom. Thus in the Cirripedia, a group containing the ship barnacles and the rock barnacles, and in the parasitic Copepoda, a group parasitic on fish, crabs, etc., the adult animal gives practically no indication of its relationships. Yet in both cases its life history shows that it is really a much modified crustacean, *i.e.* an animal allied to shrimps, etc. The sea squirts or Ascidians, almost shapeless masses of leathery jelly on the rocks, were also classified satisfactorily when their life history had been elucidated. Thus this law has aided in placing various groups in their proper position in the animal series, because their developmental history has revealed their relationship to other forms.

When there is doubt as to the exact place that any species holds in a genus, use can often be made of the fact that generally the embryos of closely related species resemble one another more nearly than those of less closely related species or than the adults themselves do. Similarly we find that embryos of closely related groups tend to resemble one another more closely than the adult members of the group.

It will be seen then that all these phenomena point to the conclusion that the present-day forms have been derived from less specialised pre-existing forms, and that from one such ancient generalised type a number of species have arisen. There is no logical reason to stop at the species, but larger and larger groups with a common structural basis have come from a more remote form, and so on.

Geographical Evidence.

On studying the geographical distribution of living beings we find that closely allied animals and plants are usually to be found living in neighbouring districts. Conversely, large tracts of land usually contain a number of allied species fairly widely scattered over it. When, however, a sea or a mountain range or a desert or some such "barrier" that has been in position for a long time, geologically speaking, intervenes, the animals and plants on the two sides of it are in general not closely related. This is because the closely allied species have had a common origin and have spread and spread until further expansion has been hindered by barriers. If closely allied species were not circumscribed in this way, and had not originated in the same place, there is no reason

why they should not appear in all parts of the world. Whereas we find in Madagascar, Australia and New Zealand, which have been separated from the nearest land for long periods of time, that they have a number of animals distinctive of themselves and not found elsewhere. In the case of Australasia we find, for example, that the lowest mammals, *Echidna* and *Ornithorhynchus*, are limited to that region and found nowhere else. When we do find species of animals that are widely spread there is an explanation forthcoming. For example, marine forms like some fish live in the sea, which does not present so many barriers as the land; or birds, butterflies, etc., being winged forms, can overcome obstacles that would prove barriers to other less easily moving forms.

Apparent contradictions to this rule are to be met with in certain groups, *e.g.* the wingless birds which appear in New Zealand (the Kiwi), Australasia (the Emu and the Cassowary), Africa (Ostrich), and South America (the Rhea or South American Ostrich); and again, the Marsupials or pouched mammals which occur in Australasia and South America. The explanation of this seeming anomaly is that both groups originated in or near the land masses of the Northern Hemisphere and spread widely, as their fossil remains show. Later on more highly developed forms appeared on the old land area, and the competition drove the earlier forms to more and more remote places. The Northern expansion was limited by climatic factors, and the result was that they were driven into the southern projecting points, where they have remained. In the case of the marsupials in Australia, the land connections broke down before the higher mammals reached it, so that the marsupials became the dominant forms. Hence we see that the apparent exceptions in reality only add a further proof of this gradual change.

Palæontological Evidence.

If evolution has actually taken place, and we could obtain specimens or records of past animals and plants, then of course we should be able to clinch the argument by showing the actual series of modifications. Such records are fortunately preserved to a certain extent in the actual remains or other evidences of pre-existing animals and plants embedded in the rocks of the earth, and to which we give the name of fossils. Had examples of all past animals been preserved, it would then be a straightforward though endless task to show how all forms were related to one another and bridge the gaps at present separating them, by intermediate forms.

A little thought will show that we cannot expect the geological record to be complete. Only a small part of the surface of the earth is possible of access, and only an infinitesimal part of this has been

thoroughly dug over and examined. Of the millions of animals that die yearly, but few are so situated at the time of their death that they can be preserved. Preservation usually takes place in a river or sea deposit or in formations like a bog. It is only the hard parts that will be preserved, save in exceptional cases, and so as a rule only those animals with hard parts are capable of leaving a record behind them. The geological record is for these and many other reasons very incomplete, but in spite of this the evidence it affords is overwhelming. We shall now examine a case in some little detail in order to see the nature of the evidence. The classical example is that of the horse, but before considering the actual details of this, we must note briefly how the records were made.

Geology, the study of the earth's crust, tells us that in remote times the land surface of the globe was composed of granites and basalts and similar hard rocks. The action of the rain, the wind, the gases of the atmosphere, etc., led to the slow breaking up of these rocks, and the loose matter was carried away by the rivers to be accumulated in layers or deposits. As the conditions under which these deposits were made varied, so the character of the layers themselves altered. We find these sedimentary rocks, as they are termed, superimposed one upon another in a succession of layers or strata. It naturally follows from their mode of formation that the lower the stratum is in a series the older it is, and also that the thickness and number of layers will give us some idea at any rate of the time taken in their formation. A number of such strata have been recognised by Geologists, and they have been divided into three main divisions or eras: the *Palæozoic,* the *Mesozoic,* and the *Cænozoic,* each representing an enormously long period of time, and each composed of a number of smaller periods. It is only the last of these, the Cænozoic or Tertiary period, that immediately concerns us, for no distinct ancestral horse form has been found prior to it. This division itself is divided into *Eocene, Oligocene, Miocene, Pliocene, Pleistocene,* and *Recent* periods, each of which is in turn composed of several distinct layers. It will be seen then that under certain conditions it is possible for an animal to be swept away and deposited by the sediment and so its bones or hard parts preserved.

The surface of the earth is constantly undergoing slow movements, whereby certain portions are subsiding and others being elevated. Sometimes this transformation, always a gradual one, takes place relatively faster than at others. In this way it comes about that the strata laid down under water get raised up to form part of the land, and they bring with them animal remains or fossils. Sometimes they are raised so high that they form mountain ranges, to become subject to the same weathering forces and so help to form further sediments.

To return now to the horse, a long series of fossil forms have been discovered, going back into the Eocene period, and these are separated up into groups of allied species, from each of which we can take as a representative a typical species. These are by no means all, but they represent so far as we know the main stages in the evolution of the horse. It is quite impossible to consider even superficially all of these or to examine all the various points of the skeletons of the forms selected. We shall consider then some of the characters of a few of the best known and striking of these stages.

Eocene.—The first animal that can be undoubtedly considered as on the ancestral line of the horse is *Eohippus*, which is found in the lower Eocene beds. It has been found both in Europe and in North America, but it is not known with certainty where it originated or what it originated from. It is interesting to note in this connection, however, that the most primitive and earliest known member of this group is *Hyracotherium*, which was found in the London clay, and is preserved in the British Museum. If it originated in W. Europe, then it must have migrated to North America, which was then entirely forest clad, across what is now Bering Strait, and in North America most of the succeeding stages were passed through.

FIG. 156.—Restoration of four-toed horse, *Eohippus*, Lower Eocene, North America.—After Lull.

Echippus was a small animal intermediate in size between, say a cat and a fox, about 11 inches at the shoulder. The fore limb had four well-developed toes with hoofs, and the fifth was represented by a splint bone, and the hind limb had three well-developed digits with hoofs, and the fourth was represented by a splint bone. The teeth indicate that it was a vegetable feeder, although they are not nearly so specialised as in the present-day horse. Its teeth and limbs throw out hints of a still more remote much less horse-like ancestor. You will see, however, that this animal does not resemble a horse at all closely, and indeed, it is highly probable that if no intermediate forms were known it would not have been regarded as having close affinity with the horse. Between *Eohippus* and *Equus*, however, are a large number of intermediate forms that grade into one another so completely that it becomes a matter of difficulty to draw a line between one species and another.

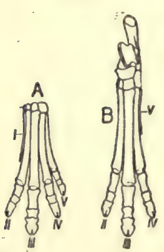


FIG. 157.—Hand (A) and foot (B) of *Eohippus*. One-fourth natural size.—After Marsh, from Lull.

Later, in the middle Eocene, appeared *Orohippus*. This form

shows a distinct increase in size, and was about 14 inches at the shoulder, and in size and proportions resembled a whippet. The fore foot had lost all trace of the first digit, and the hind foot all trace of both the first and the fifth digit. In addition to this, certain alterations are also observable in the teeth.

Oligocene.—In the lower formations of this period appeared

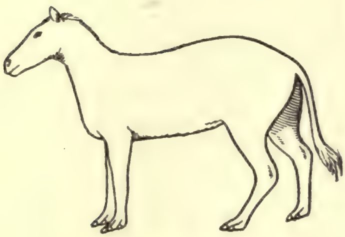


FIG. 158.—Restoration of four-toed horse, *Orohippus*, Middle Eocene, Wyoming.—After Lull.

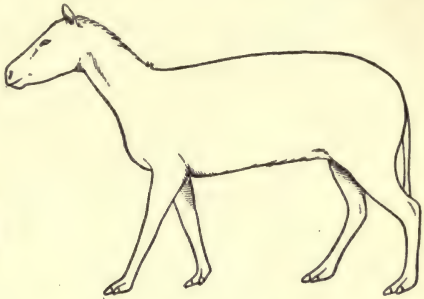


FIG. 159.—Restoration of three-toed horse, *Mesohippus*, Middle Oligocene, North America.—After Lull.

Mesohippus, which was a slightly larger animal, about 18 inches high at the shoulder. This is known as the three-toed horse, because in the fore foot the fifth digit was present only as a splint bone and therefore quite rudimentary, while the hind foot remained much as before. Thus both fore and hind feet possesses three toes with hoofs.

Miohippus was a still later three-toed horse, from the Upper Oligocene beds. It represents an advance in size on Mesohippus, being 24 inches high at the shoulder, *i.e.* about as large as a sheep. In its skeleton it is not much more advanced save that the splint of the fifth digit is in a still more rudimentary condition. Both types had the middle digit larger than the lateral digits, indicating that it was the most important in locomotion, and in both also the teeth show some advance in complexity.

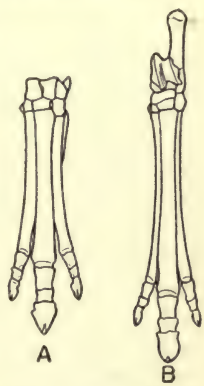


FIG. 160.—Hand (A) and foot (B) of *Mesohippus*. One-fourth natural size.—After Marsh.

Miocene.—This period also furnishes a group of horse-like forms. *Miohippus* continues over into the lower formations, while in the middle formations we find *Parahippus* and *Hypohippus*. These are types which, while showing certain advances in size, etc., also indicate specialisation

in the directions of becoming forest dwellers. On the other hand, *Merychippus* from the middle and upper layers, while it also shows a slight increase in size, is more important in that it is modified for a life on the plains. Its permanent teeth are adapted for a grass diet, while its milk teeth still retain the characteristics

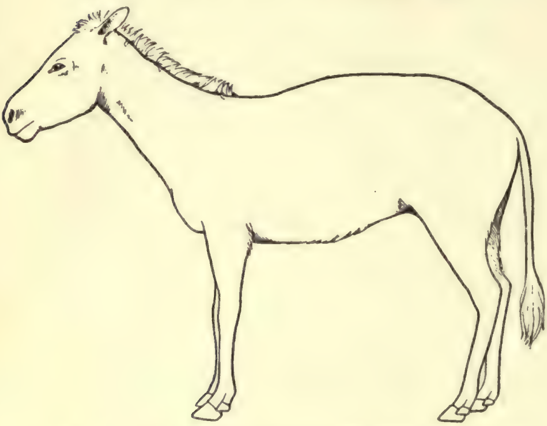


FIG. 161.—Restoration of the Miocene prairie horse, *Merychippus*.—After Lull.

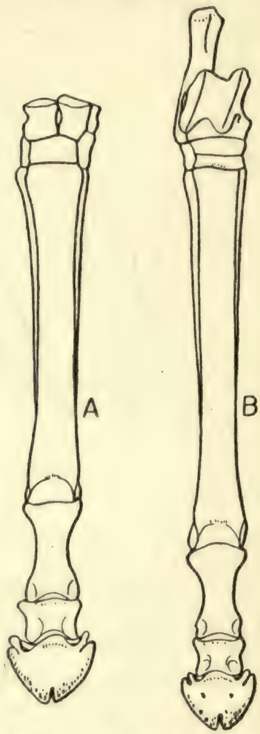


FIG. 162.—Hand (A) and foot (B) of the first one-toe horse, *Pliohippus pernix*, Pliocene, Nebraska. One-fourth natural size.—After Lull.

of an animal feeding on shrubs and softer vegetation. Further, while still three toed, in ordinary locomotion its lateral digits did not reach the ground. In the upper Miocene appears *Protohippus*, which stood 36 inches at the shoulder. There is not much structural advance shown save that the lateral digits are slightly smaller and further removed from the ground. The principal point of interest is the teeth, whose enamel has become more complex, and even the milk teeth are of the grass-eating type.

Pliocene.—This period is represented by *Pliohippus*, which first occurs in the middle beds. It was 48 inches at the shoulder, a fairly large modern horse being 60 inches, *i.e.* 14 hands, and was more horselike in its general proportions. In this animal the two lateral toes on fore and hind feet become more reduced, and in some of the species have almost entirely disappeared, or better become nearly as rudimentary as in our modern horse.

Pleistocene.—Finally, in the lower Pleistocene appeared the genus *Equus*, the relatives of our modern horse, and represented by numerous skeletons of *E. Scotti*. It is, as is known, one of the best-adapted animals for locomotion by means of running that we know, and is marked off from all other living genera by the fact that it possesses but a single toe on fore and hind feet. The relics of the next two lateral bones are to be found as a pair of splint bones, remains of metacarpals. At present there are three main types of the horse family found wild in the world, known as horses, asses, and zebras. They are mainly to be distinguished by external characters, and their skeletons are remarkably alike.

The slow development of the horse from the "dawn horse" *Eohippus* of the early Eocene up to the appearance of the modern genus *Equus* was contemporaneous with the disappearance of much of the forest land in North America and its gradual replacement by the plains and prairies we now find there. From a wood dweller the horse gradually become fitted for a life on grassy plains, from an animal with teeth for browsing on herbs and shrubs to one with teeth for grazing on grass. The specialisation not only affected the feet and size of the body, but the whole structure of the horse including the head. This alteration is particularly noticeable in the Miocene times, when much of North America became grass land and several types suited to grazing appeared and also became extinct.

Throughout the Pleistocene times horses of the genus *Equus* are to be found in North America, where the genus was apparently widespread and numerous. Every now and again from Oligocene times horses reinvaded Europe, as the discovery of their fossil remains testify, but they do not appear to have flourished there as they did in North America. Strangely enough, however, during the Pleistocene period the invasion was successful, and the genus *Equus* became very widespread over the plains of Eurasia. For some reason at present unknown, horses died out completely at a subsequent period in America, which became isolated from Asia by the breakdown of the land connection and the formation of Bering Strait. All the herds of horses, the mustangs, found all over the prairies of North America by the early colonists are due to horses re-introduced in historic times. They are the descendants of the horses that escaped from the old Spanish explorers. The disappearance of the original species of *Equus* in North America is all the more remarkable since on the re-introduction of the same genus they flourished so well.

This past history of the horse at which we have only briefly glanced is undoubtedly one of the most complete, but it is paralleled by that of other groups, *e.g.* the elephant, the rhinoceros, the camel,

ERAS	EPOCHS Indicating approximately relative duration as estimated by thickness of deposits	Range of Animal Groups							Probable dominant form of Animal Life.
		Invertebrates	Fishes	Amphibia	Reptiles	Birds	Mammals	Man	
CAINOZOIC or TERITARY	Recent & Pleistocene 4,000 ft.								Age of Man.
	Pliocene 13,000 ft								Age of Mammals
	Miocene 14,000 ft								
	Oligocene 12,000 ft.								
	Eocene 20,000 ft.								
MESOZOIC or SECONDARY	Cretaceous 44,000 ft.								Age of Reptiles
	Jurassic 8,000 ft.								
	Triassic 17,000 ft.								
PALAEOZOIC or PRIMARY	Permian 12,000 ft.								Age of Amphibia
	Carboniferous 20,000 ft.								
	Devonian 22,000 ft.								Age of Fishes
	Silurian 15,000 ft.								
	Ordovician 17,000 ft.								Age of Higher Invertebrates
	Cambrian 26,000 ft.								
PRE-CAMBRIAN (*Proterozoic & Archeon*) Extent not Known									

FIG. 163.

etc., etc. In each case they can be traced back to more primitive, less specialised forms.

These cases are, however, specific instances, but when we turn to the general evidence from palæontology we shall find that it is just as strong. Let us glance for a few moments at the sequence in which the various classes of the Vertebrata appear ; but in order to do so we must first fill in the subdivisions of the other two geological eras (*vide* diagram). Throughout the whole of the Archæan or Proterozoic and major part of the Cambrian we find no trace of any animal with a vertebrate structure. They first appear possibly in late Cambrian, but certainly in the Silurian, and these are the fish. In the next period, the Devonian, we get more fish and the earliest, most primitive Amphibia, and soon after in the Carboniferous other and more highly developed Amphibia and very primitive amphibia-like reptiles. The Permian period saw the origin of a number of new and more developed Reptilia, which however increased greatly in variety and organisation, so that they were the dominant forms during the greater part of the Mesozoic Era, which is in consequence termed the " Age of Reptiles." One line of reptilian development led in the upper Triassic to the primitive Mammalia. These are undoubted mammals, and the group has gradually gone on, and in the Cænozoic Era it replaced the Reptilia as the dominant group. The culminating and most recent addition to the Mammals is man himself, who first appears in the Pliocene period. With the spread of our knowledge of fossil forms that has taken place in the last twenty or so years, it has been increasingly difficult to separate off the Reptilia from the Amphibia on the one hand and the Mammalian on the other.

The birds appear as a highly specialised offshoot from the reptiles in the Jurassic, which also furnishes us in its early layers with that remarkable mixture of bird and reptile Archæopteryx.

This short account suffices to show the kind of evidence that we derive from Anatomical, Embryological, Geographical and Palæontological sources. The amount of evidence that has now been amassed is colossal, and it is being added to year by year. It all points most clearly to the fact that living matter was at first simple, but through countless ages it has gradually become more and more specialised and produced an endless variety of forms. This long-continued and continuous process of change or Evolution has resulted in the production of all the many animal and plant forms at present inhabiting the earth.

Darwin.—The most masterly contribution to the subject of Evolution was not made until fifty years after the appearance of Lamarck's book, when Charles Darwin published his " Origin of

Species" in 1859. This immortal work gave the first satisfying and truly scientific account of the process of organic evolution, and further tried to account for the manner in which it is brought about in nature. The theory of Natural Selection, as it is called, was first conceived by Darwin in 1838, but it was not until he had given the matter twenty years' further thought that he published a paper conjointly with Alfred Russel Wallace in the *Transactions* of the Linnæan Society, and followed it a year later by his book. A. R. Wallace was a younger biologist working in Melanesia, who quite independently arrived at conclusions very similar to Darwin's. This joint publication was the beginning of a life-long friendship between these two great men.

Charles Darwin was born, strangely enough, in 1809, the year of the publication of "Philosophie Zoologique." In 1825, he went to Edinburgh to study medicine; he stayed about two years, and in 1828 went to Cambridge. He was appointed naturalist to the *Beagle* in 1831, and went on a voyage round the world in her that lasted till 1836. This voyage played a great part in shaping his ideas, and he has left a charming account of it in "The Voyage of the *Beagle*." In addition to writing "The Origin of Species," Darwin did an enormous amount of biological work. "The Origin of Species," or, to give it its full title, "The Origin of Species by means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life," is a book that has probably influenced human thought more than any other, and certainly was the foundation stone of modern biology. We must consider briefly its main points.

The tripod upon which this theory rests are the three factors Variation, Heredity, and the Struggle for Existence, and we must glance briefly at the meaning of each of these.

Variation.—Variations are extremely well known in our domestic animals and plants, for no matter how much the offspring may resemble the parents it is never precisely the same. The various members of one family are not absolutely alike. By recognising and taking advantage of these variations man has been able to achieve much. Thus, probably all the various species of cabbage, cauliflower, broccoli and Brussels sprouts, etc., are derived from the one wild species *Brassica oleracea*. In the same way apples, of which we now grow about 1000 varieties, come from the wild crab apple. The standard examples in the animal kindgom are the various kinds of pigeon (*Columba livia*), of dogs, cattle, etc. In all these cases the result has been attained by selecting and breeding from the forms with the desired characteristics. As it has been done intentionally by man in gardens or breeding pens it has been termed "artificial selection." A similar kind of variation is to be seen in all living ani-

mals and plants under natural conditions. No two members of the same species are absolutely alike; they vary in size, shape, colour, relative size of parts, and so on. Not only is this true of the external features, but it applies also to the various internal organs. All parts of animals vary to some extent, and while in some cases it is more apparent than in others, it is almost always possible to measure this variability. This statistical investigation of the phenomenon of variation was started in England by Francis Galton and continued by Professors Karl Pearson and Weldon.

Let us take an example or two.

A collection of a large number of beech leaves was made at random and the number of main veins coming off from the mid rib counted, and the following result obtained:—

No. of veins	10	11	12	13	14	15	16	17	18	19	20	21	22
No. of leaves	1	7	34	110	318	479	596	516	307	181	36	15	1

This may also be expressed in the form of a curve with the number of veins on the abscissa and the number of leaves on the ordinate.

A similar series of measurements have been made on men, *i.e.* the height of 4426 members of the University of Cambridge of British extraction. The result is shown in the accompanying diagram, where the stature in inches is on the abscissa and the number of individuals on the ordinate. The diagram also shows the curve that most nearly fits the points obtained. (Such a curve is known as a normal curve, and is expressed mathematically by the equation $y=e^{-x^2}$.)

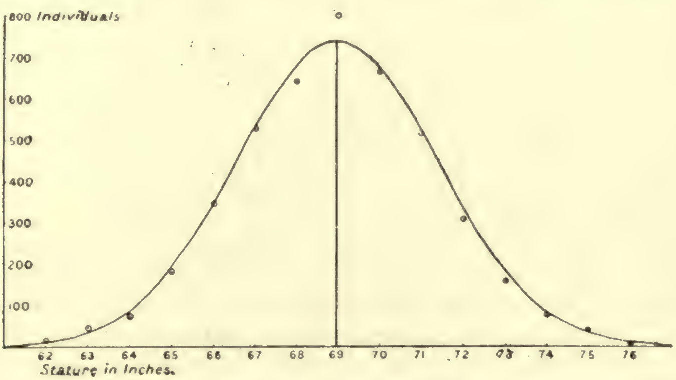


FIG. 164.—Curve of heights of undergraduates of Cambridge University of British extraction.

The line from the base to the highest point is termed the **mode,** or in other words the mode is the point at which the largest number of individuals occur, and often the curve balances on each side. Sometimes the curve is asymmetrical because the variation is more limited on one side than the other. This is termed a skew curve.

Heredity.—Heredity is the second great factor. At the commencement of the life of one of the higher animals we have the fertilised ovum. This is derived from the union of the sperm, a part of the male parent, and the ovum, a part of the female parent. As we have seen, each parent contributes an equal number of chromosomes to the nucleus of the new organism and these it is that are the important structures in controlling the course of development. Because of this relation to its parents the offspring resembles them, and we give the name "heredity" to the genetic relation between parents and offspring. The inheritance of an animal, then, is all that it possesses in virtue of its relation to its parents. This relationship has long been recognised and is expressed in a number of popular sayings, such as "like begets like," "a chip of the old block." That the heritage or inheritance is also generally recognised as important is expressed by the old adage, "You cannot make a silk purse out of a sow's ear." The power of handing on characteristics is one of the necessary conditions of evolution; without it evolution could not have taken place.

Francis Galton in 1897 formulated what is known as "Galton's law of ancestral inheritance." He says, "the two parents contribute between them on the average $\frac{1}{2}(\cdot 5)$ of the total heritage of the offspring; the four grandparents $\frac{1}{4}(\cdot 25)$; the eight great-grandparents $(\cdot 125)$; and so on. Thus the sum of the ancestral contributions is expressed by the series $\cdot 5$, $(\cdot 5)^2$, $(\cdot 5)^3$, which being equal to one accounts for the whole heritage." Professor Pearson's work leads him to conclude that the series would be more accurately expressed by ·6244, ·1988, ·0630, etc., but this does not affect the validity of the law; it only indicates that the actual contribution of the immediate parents is somewhat higher than Galton estimated. It should be noted that Galton's law is a statistical law giving the average result of the analysis of large groups, and does not necessarily apply to the inheritance in any one individual case.

Selection.—We have seen what is meant by Variation and Heredity, and now pass on to consider the third factor, Selection, to the action of which the other two are necessary conditions. This is also termed the Struggle for Existence, and was arrived at firstly by a consideration of the manner in which animals multiply.

Darwin's own classical example is that of the Elephant, one of the slowest breeding of all animals. We may assume as fairly

probable that the elephant does not breed before the age of 30 years, and continues to do so, excluding accidents, till 90 years of age. Let us further assume that during this period six young are born. You will see that this by no means over-estimates the possibility and is a very slow rate of multiplication; yet in 740 or 750 years, a mere nothing in the history of the earth, there would be 19 million living descendants of the first pair. Professor Punnet was engaged in breeding Rotifers, very tiny animals not much larger than Paramœcium, and found that each female produced 30 eggs at a time, and 67 generations were obtained in less than a year. Had he been able to keep all the animals alive, by the end of the year they would have formed a solid mass many times larger than the earth. To take an example from plants, Professor Buller has estimated that the giant puff ball produces 7,000,000,000 spores, so that in two generations there would be a mass of puff-balls 800 times the volume of the earth. These are, of course, impossible happenings, for there is always a heavy mortality, but they serve to illustrate the fact that living organisms reproduce comparatively rapidly, and in a geometric ratio, so that in time their number would be infinite.

A rough measure of the amount of mortality may be arrived at in the following way. We have no reason to suppose that the number of codfish is more to-day than it was, say, 50 years ago. Each pair of cod may lay 9,000,000 eggs in a year, and will continue to do so for a number of years—let us say five, although actually it is more than that. But as there is to be no increase, then of the 45,000,000 possible codfish from the original parents only two survive to replace them.

This is but one example, and it is paralleled by many others. The great loss of life incidental to any great war is nothing to the colossal slaughter that is carried out in the course of nature every day. Nature is absolutely relentless in her annihilation, and those who talk of the perfection of nature do not always realise the price that is paid for that perfection.

The method in which this destruction takes place can easily be conceived. We see that if we consider an imaginary example of animals in a new country, say, for example, an island. At first all will be well and they will flourish; before long, however, the food, supposing the supply to be constant, which was ample for the few, is only just sufficient to go round. This stage may be called one of Equilibrium, and after it has been passed the problem of obtaining food becomes serious. Obviously, if there is only food enough for 100 animals, then all above that number must be starved out. Which ones are to be starved? "The race is to the swift and the battle to the strong." Those animals that cannot run so well,

fight so well, see so well, are not so cunning, etc., will be exterminated ruthlessly. The more animals produced the more fierce this "struggle for existence" and the larger the number of individuals blotted out, and we can see that this all becomes intensified if, instead of the simple case imagined, we have, as we have in fact, large numbers of different animals on the same area.

The whole of the external surroundings of an individual, the earth or water, the other animals, the plants, the climate, the weather and all the many factors of the external world that affect an animal even in the remotest way, we include in the one term **"environment."** Thus the environment of an animal is every external influence that plays upon it from the moment it starts life as a fertilised egg until its death. In order to survive in the struggle for existence the animal must be suited to its surroundings in its structure and habits. Thus it would be useless for a cat to develop a fin unless it at the same time altered its mode of life, and so on. We put this in another way by saying that an animal must be "adapted to its environment." A character or structure is called adaptive when it is of obvious use to the possessor. An animal that is well adapted to a certain environment is said to be fitted to it. Note the scientific use of the word "fit," so often misunderstood or misused in popular writings. When we say an animal is "fit" we imply no physical, mental or moral superiority whatever; we simply mean that it is adapted to its environment. Should the environment change, the animal that was fit probably becomes unfit. We have realised that in the struggle for existence it is the unfit that are eliminated, and so indirectly the fittest are selected. Hence the philosopher Herbert Spencer, who arrived at much the same conclusions as Darwin from more theoretical reasoning, termed natural selection "the survival of the fittest."

Thus we have glanced quite briefly at the three main factors that Darwin recognised, Variation, Heredity and Natural Selection.

The struggle for existence is not so simple a process as we assumed in the imaginary example of the animals on the island, and various entirely different forms have an enormous indirect influence and dependence upon one another. To illustrate this we may take two well-known examples. It is not at first sight obvious why the crop of red clover (*Trifolium pratense*) should be in any way dependent upon cats, yet it is to a certain extent. Red clover is fertilised almost entirely by bees; the number of bees in a neighbourhood (excluding carefully guarded hives) depends on the mice, which destroy the bees' nests, eggs and young; the number of mice is largely kept down by cats (owls also play a part).

Many years ago goats were introduced into St. Helena, which

was well wooded. They destroyed all the forests by eating up the seedlings as they appeared. With the forest disappeared also the birds and insects living in them, insect-fertilised flowers were also affected, and, indeed, even the climate was changed.

The argument set out in the Origin of Species may be briefly summarised by what is known as Wallace's chart :

Fact.	*Consequence.*
A. Rapid increase in numbers B. Total number of species stationary	Struggle for Existence.
C. Struggle for Existence D. Variation with Heredity	Survival of the Fittest.
E. Survival of the Fittest F. Change of Environment	Structural modification and differentiation of species.

Darwin's own conclusions on the matter are best summarised in his own words. "I have now recapitulated the facts and considerations which have thoroughly convinced me that species have been modified, during a long course of descent. This has been effected chiefly through the natural selection of numerous slight, favourable variations ; aided in an important manner, that is, in relation to adaptive structures, whether past or present, by the direct action of external conditions, and by variations which seem to us in our ignorance to arise spontaneously. It appears that I formerly underrated the frequency and value of these latter forms of variations, as leading to permanent modifications of structure independently of natural selection."

Here then we have a statement of the case as Darwin conceived it, and in it we have the phenomena of evolution definitely envisaged and set forth. This was done so successfully that it has never been seriously doubted since, and herein lies Darwin's great service to Biology. He put forward an enormous amount of evidence demonstrating evolution in such a cogent manner that even the most sceptical were convinced. With it he also proposed a *theory* to account for the causes responsible for evolution, which is quite logical and conceivable. The Biologist, however, is not entirely concerned with logical possibilities, and he desires to know if this is *actually* the way in which evolution was brought about. Herein, as pointed out previously, subsequent workers have not always agreed with Darwin.

The publication of the "Origin of Species" exerted a profound influence upon biological work, and marked a complete change in the scientific outlook.

Post-Darwinian Biology.

Darwin and his contemporaries admitted that Lamarck's "use inheritance" probably played some part in the formation of new species, though in the main this was due to the action of natural selection. Herbert Spencer upheld this view strongly, and perhaps A. R. Wallace alone opposed it.

The first naturalist to oppose it in a very thorough way was August Weissmann, who, in a long series of publications starting in 1885, denied all transmission of what he termed "acquired characters." Acquired characters he defined as "those which result from external influence upon the organism, in contrast to such as spring from the constitution of the germ." In other words, "Modifications which are wrought upon the formed body, in consequence of external influences, must remain limited to the organism in which they arose. No such modifications of the same can be transmitted to the germ cells from which the next generation springs." These

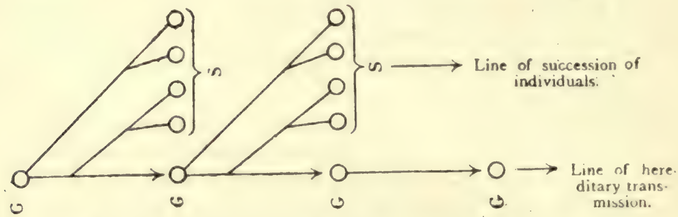


FIG. 165.—Diagram to illustrate the idea of continuity of the germ plasm.

conclusions were reached, firstly, as a result of the exhaustive study of all the instances in which such transmission was alleged to occur. He was able to show that none of these cases furnished evidence of a definite and incontestable character. Secondly, he made a study of the mechanism whereby any characters could be transmitted. As a result of these researches, Weissmann elaborated a series of doctrines, known collectively as Weissmannism, the principle of which is that of "the continuity of the germ plasm." According to this theory, we must regard the offspring as inheriting from the germ cell of the parent and not from the body of the parent. In support of this, it is urged that in some animals one of the very early blastomeres is definitely set aside as the producer of the germ cell, and develops more or less independently of the rest. In still more cases the germ mother cell is recognisable at a very early stage, as we have seen in *Obelia*, and, finally, in almost all the remaining animals the primitive germ cells are formed before the appearance of discrete organs. So that the body, as it were, acts as a guardian

and trustee for the germ cells, and this idea may be expressed roughly by a diagram. Weissmann points out that no satisfactory way has been discovered whereby a subsequent alteration in such organs could conceivably influence the germ cells from which they have long been dissociated. Many modern Biologists are in general agreement with this view, which they claim is supported by the evidence of recent cytological and embryological investigations, but there are others who disagree. These latter do not indeed hold to the crude doctrine of " use inheritance " as propounded by Lamarck, but maintain that a changed environment will after a certain number of generations impress itself on the germ cells and bring forward a certain amount of experimental evidence to support this. One of the best known of these is Tower's work on breeding beetles of the genus *Leptinotarsa* under different environmental conditions, and noting the effect upon the offspring. The subject is too wide to be pursued further, but is one that has received a great deal of attention, and much of the discussion it involved has been concerning the use of words rather than the import of the evidence considered.

All these works, especially that of Darwin, caused a great deal of attention to be paid to these questions, and, in particular, led to a large number of investigations of the problems of heredity along different lines.

One of the most striking papers was that of Mendel, which was published in 1866, and was not a result of previous activities. It was, however, entirely overlooked, and its significance not appreciated, owing to the discussion aroused by the " Origin of Species." The paper was not heard of until it was rediscovered independently, and practically simultaneously by three separate workers, Correns, Tschermak, and de Vries, in different countries early in 1900.

Johann Mendel read his two papers to the Natural History Society of Brunn, where he was a priest, and soón after, unfortunately for his scientific work, he was made Prälat of the monastery of Brunn. Let us examine some of his actual experiments. He crossed various varieties of peas, differing in certain points, and observed numerically the result of breeding from these crosses. Seven pairs of characters were investigated, but it is only necessary to consider two here. Firstly, the seeds of different plants were found to be more or less round and smooth, or irregular and deeply wrinkled. Secondly, the seeds were noticed to be either yellow (or orange) or green. In both cases the result was the same as that in the following account where only the characters, smooth and wrinkled, are considered, and it would still be accurate if yellow were substituted for smooth, and green for wrinkled.

Plants bearing smooth seeds were crossed with those bearing wrinkled seeds, and the results obtained can be expressed diagrammatically. In the first filial generation (F. 1), all the peas were smooth, and the wrinkled character had disappeared. When members of this generation were interbred, however, it was found that in their offspring, the second filial generation (F. 2), wrinkled

S X W

F. 1. (S)

F. 2. S (S) (S) W

seeds again made their appearance, and in the proportion of 1 wrinkled to 3 smooth. It is interesting to recall the actual results obtained by Mendel to see how closely they agree with the proportions given: 258 plants yielded 8023 seeds, 6022 yellow and 2001 green; their ratio, therefore, was 3·01 to 1; 253 plants yielded 7324 seeds, 5474 round and 1850 wrinkled; their ratio was, therefore, 2·96 to 1. Further investigation showed that the three plants with smooth seeds did not all behave in the same way. One of them was similar to the smooth-seeded plants with which we started, and if inbred would never produce anything but smooth seeds, no matter how many generations were tried: it was, as we say, "**pure.**" The other two behaved similarly to that of the F. 1 generation, and of their offspring one-third always produced wrinkled seeds, so that they were impure. The true ratio then of the plants in the Fig. 1 generation is 1 : 2 : 1. For a character that we can examine in this sort of way the term "**unit character**" is employed, and when we find a pair of such characters that are mutually exclusive, they may be termed "**allelomorphs,**" as they were called by Bateson. Mendel, in order to describe the masking that occurs in the F. 1 generation,

D X R

F. 1. DR

F. 2. D DR DR R

proposed the term dominant for that character that appears in the F. 1 generation, and recessive for the one that does not, so that we can express the result in a generalised diagram. This result is sometimes referred to as Mendel's Law of Dominance, although it is not, strictly speaking, a law, since it is not of general application,

and in many crosses we get a condition intermediate between the parent forms.

What is the explanation of this phenomenon ? In the first place, it is obvious that the germ cell of the parent may be considered to carry something which we term a **factor,** let us say D or R, that determines the appearance of the character in the next generation. If there were a complete blending of these characters in the F. 1 generation, then we should expect all the F. 2 and subsequent generations to remain the same, but they do not. Suppose we imagine two sorts of pollen grain to be produced in the Fig. 1 generation, one with the factor D and the other with the factor R, and in the same way two sorts of ovules. We can easily see all the chance combinations possible and the result.

D	may	fertilise	D	giving	DD
D	,,	,,	R	,,	DR
R	,,	,,	D	,,	RD
R	,,	,,	R	,,	RR

This is the proportion that we actually do get, and so it seems the reasonable explanation. That is to say, in the germ cells of the F. 1 generation the unit characters are not blended, but segregated in different cells, a phenomenon that we term **segregation.** It can be checked by the consideration of other cases, *e.g.* suppose the F. 1 generation, *i.e.* DR, be back-crossed with the parent R, then we get offspring in the proportion 2DR : 2RR, exactly what we should expect. To take a more complicated example, suppose we cross a green smooth pea with a yellow wrinkled seed. The F. 1 generation is smooth, as this is dominant to wrinkled, and it is yellow, as this is dominant to green. Thus we can represent this diagrammatically :

$$
\begin{array}{ll}
 & \text{Sg} \times \text{wY} \\
 & \quad\downarrow \\
\text{F. 1.} & \text{SwYg}
\end{array}
$$

Now if we consider the possible ways in which these factors can be segregated in the gametes of the F. 1 generation we shall find it is four, namely, SY, Sg, wY, and wg. The possible combinations of these gametes can be seen if we place them along the sides of a square and then divide the square up into 16 smaller squares. In each square of the vertical columns place the symbols above the column, and in each square of the horizontal rows place the symbols at the beginning of each row. The squares then indicate all the possible fertilisations from gametes that are so constituted. It will be seen that in 9 squares the letters S and Y occur ; in 3 squares the

letters Sg; in 3 the letters Yw, and one only contains nothing but wg. Since smoothness (S) and yellowness (Y) are dominants, the result of the cross will be 9 plants bearing smooth yellow seeds, 3 bearing smooth green seeds, 3 bearing wrinkled yellow seeds, and 1 bearing wrinkled green seeds. This result has been approximated to quite closely in experimental results.

	SY	Sg	wY	wg
SY	SY SY	Sg SY	wY SY	wg SY
Sg	SY Sg	Sg Sg	wY Sg	wg Sg
wY	SY wY	Sg wY	wY wY	wg wY
wg	SY wg	Sg wg	wY wg	wg wg

Two other terms are used to indicate certain kinds of individuals. The gametes or germ cells are always pure for certain factors, but the zygote or individual is not. It may be pure with regard to a certain character, say D, when we say it is a **Homozygote.** On the other hand, it may be impure as in the F. 1 generation, in which case we say it is a **Heterozygote** with regard to that particular pair of allelomorphs. A Homozygote produces gametes all bearing the same factor, a Heterozygote produces gametes bearing different factors. Lastly, because of the way in which the recessive character disappears in the F. 1 generation in many of the crosses made and then reappears again in the F. 2 generation, this particular type of **inheritance** is called **alternate**, but as noted above this phenomenon is by no means always manifested in crossing.

The great value of Mendel's work and of its rediscovery was not merely in the actual facts it brought to light, but in the stimulating effect it had upon the experimental investigation of the problems

of heredity; suggesting the lines of work and also the technical methods to be employed. Numerous investigations have been made along these and similar lines, and many useful results achieved; to some of them we shall return later. It cannot yet be said, however, that Mendelism has supplied the key to all problems in heredity, and it would appear that certain characters so far have not been analysed in Mendelian terms. Before considering the direct extension of Mendel's work we may turn aside to consider two other discoveries.

An important contribution to our knowledge of heredity was made by de Vries, one of the rediscoverers of Mendelism, whose important book, "The Mutation Theory," was published in 1903. This author found wild in a potato field hundreds of specimens of the evening primrose *Œnothera lamarckiana,* which seemed to exhibit more than ordinary variability. These he removed to the gardens at Amsterdam and bred carefully. In a few years he found he had produced seven distinct types, "elementary species," as he termed them, all so different from the original that each would have been described as a new species had it been found in Nature. Moreover, he found that each of these would breed true to type generation after generation. The most remarkable point about them was that they appeared suddenly and without warning and then persisted. They were so different from the original that they would find no place in the normal curve of the species. For these suddenly arising but persistent forms de Vries proposed the name **mutant,** and the process was described as **mutation.** The cause of these mutations is practically unknown, and although there has been much theoretical speculation concerning them we have not time to enter into it here.

It is quite clear from this, however, that we shall have to reconsider what we mean by variation. We have seen that ordinary variations may be expressed by a normal curve, but these are variations about a mean, and no amount of breeding from among them would produce forms outside the limits of the curve. For such variations, which may be described as "normal variations," the more strict term "fluctuations" has been proposed. Against these we may set the mutations of de Vries. The term "variation," then, as it was used, and as we first used it, included both fluctuations and mutations, and, according to de Vries, it is only the selection of the latter that can have led to the appearance of new species.

Further interesting observations were made by Professor Johannsen, who investigated the phenomenon known as the **"pure line."** He found in beans, where self-fertilisation is possible, that all the descendants of a single plant showed normal variation about a certain type. This type need not be the same as the type for the general population of all beans of the same species. Moreover, if

one of the extreme variants of this subsidiary type were taken, its offspring showed regression to the type of the line not the type of the species. He defined as a **"pure line,"** therefore, a group of individuals which has a normal variability of its own, and the offspring of which by self-fertilisation breed true to the type of their own particular group. A result of this is to show that selection in a population will come to an end when you have been able to separate out the most eccentric line. Further progress must be made by utilising mutations or dealing with the characters in a Mendelian manner. This phenomenon of a pure line is of considerable practical importance to the breeder of plants.

To return again to Mendel's work, we find that we can deduce from his and similar experiments two general principles. The first is, that whatever unit factors may be introduced into the zygote at fertilisation, such factors are not completely blended, but are sorted out again in the gametes it produces. This is termed the law of **segregation.** The second is, as we have seen when considering the behaviour of two pairs of unit characters, that the inheritance of each pair of characters is independent of the other. This is known as the law of **independent assortment.** As was noted above, the rediscovery of Mendel's work served as an inspiration to further investigation along similar lines, and many fruitful fields of research were opened up. One of these that is particularly associated with the names of Morgan and his fellow-workers is of interest, since it is in the main a direct extension of Mendel's own experimentation, and has yielded additional laws. In the first place, it has been found that the second law given above is not of universal application, and that, while it is true in quite a number of cases, an ever-increasing number of examples are found in which there is a marked tendency for groups of characters to be inherited together from generation to generation. This tendency to keep together, so that it is really the groups that are independently assorted rather than the individual characters, is termed **linkage,** and it is obvious that this limits the law of independent assortment. There are certain theoretical points that can be advanced to explain this apparent contradiction. We have reason for thinking that the chromosomes are the actual bearers of the factors whose presence in the zygote is necessary for the appearance of certain characters in the adult. Moreover, the chromosomes retain their identity from division to division, and the factors are related to them in a very intimate and individual manner, and not in a loose general way. We should expect, therefore, that the character groups correspond with the chromosomes. In support of this, we find that in *Drosophila melanogaster*, the vinegar fly, there are as many groups as chromosomes, the three largest con-

sisting of at any rate 100, 75, and 60 factors, and one small group is intimately associated with sex inheritance and depends upon the presence of a certain small "sex chromosome." Furthermore, up to the present no species has been found in which the number of linked groups exceeds the number of chromosomes. When this is taken into consideration, therefore, we find that the second law should read that groups of characters tend to keep together—this is linkage—but that the pairs of groups may be assorted independently. Thus the explanation of Mendel's apparently contradictory result is that he happened to choose factors that belonged to separate groups.

The linkage of these large groups is not absolute, and while on the whole the members of one group tend to keep together, yet in a certain percentage of cases in some of the crosses it is clear that a small group from each one of a pair of large groups interchanges. This can be represented diagrammatically as follows: suppose the allelomorphic factors of the original large linked group to be represented by letters:

A, B, C, D, E, F, G, H, I, J, K, L,
a, b, c, d, e, f, g, h, i, j, k, l,

Then in a certain percentage we shall find that in the formation of the germ cell, equivalent groups from each have interchanged (as evidenced by the appearance of the corresponding factors in the zygote) thus:

a, b, c, d, E, F, G, H, I, J, K, L,
A, B, C, D, e, f, g, h, i, j, k, l,

As a rule, the percentage that do this is small, though sometimes it may reach as high as 33 per cent.; in such cases we say that the two groups at the beginning were loosely linked. It should be borne in mind, however, that the exchange takes place between allelomorphic factors in homologous large groups—the exchange is not haphazard, but exact; and also that the percentage of cases in which it occurs is definite in all crosses for the same group of factors. This phenomenon is termed "**crossing over,**" and is, as it were, an addendum to the law of linkage, which can be correspondingly modified to state that while groups tend to remain linked in inheritance, yet in some cases a definite amount of crossing over may occur. Without entering into a discussion of the subject, it may be noted in passing that there is a possibility of such an exchange taking place during the synapsis stage of maturation when the two halves of a bivalent chromosome may be twisted around one another to a greater or less extent.

When the numerical results of a series of matings in which

crossing over occurs are investigated, it is found that there is a very definite relation between the percentage of crossing over in groups containing a certain number of common factors. Let us consider an imaginary example. If *a* is a factor that is usually linked with a group, but sometimes crosses over, then we might find in a cross that *a* would remain linked with the group in 95 per cent. of the cases, while it would cross over in 5 per cent. Thus we could term 5 the cross-over value and 95 the linkage value. Suppose, further, that in crossing over *a* is sometimes accompanied by other factors, *b* and *c*, then of course there would be a cross-over value for each combination. Suppose the cross-over value of the pair *ab* is 5 and of *bc* is 10, both pairs containing a common factor *b*, then we shall find that the cross-over value of *a-c* is either a function of the difference between the values of *ab* and *bc*, *i.e.* 5, or a function of their sum, *i.e.* 15. This is so unless the results are interfered with by some other phenomenon, and it is a condition that, as may be seen, would follow if the factors were regarded as three points on a straight line. If we take four factors or five factors, and so on, this inter-relationship still holds good, and, again, this is readily comprehensible if they are arranged in a straight line. Thus we can deduce a further generalisation of the inheritance of factors, namely, that such factors, responsible for the production of certain characters, are arranged in a linear order. This is sometimes referred to as the law of the **"Linear order of the factors."** It should be noted that this result follows from an analysis of the mathematical results obtained by experiments, and is independent of any consideration of chromosomes, etc., but nevertheless it is obvious that the chromosomes and their behaviour in maturation and fertilisation provide a good mechanism by means of which we can conceive that such a linear arrangement of the factors with its attendant phenomena could easily be carried out.

We may here leave the question of hereditary relationship between parent and offspring and return to the more general question of the manner of evolution of the various forms of life by considering the outlines of the past history of one group of animals as far as it has been revealed by Palæontology. For an example we shall take the Class REPTILIA, since they are fairly well known, and from them have sprung the higher vertebrates living in the world to-day.

Somewhere near the middle of the Devonian period the primitive pentadactyl Vertebrates had already appeared on the Earth. Various authorities have calculated how long ago this was, and arrived at very different estimates, but even low ones give it as over 20,000,000

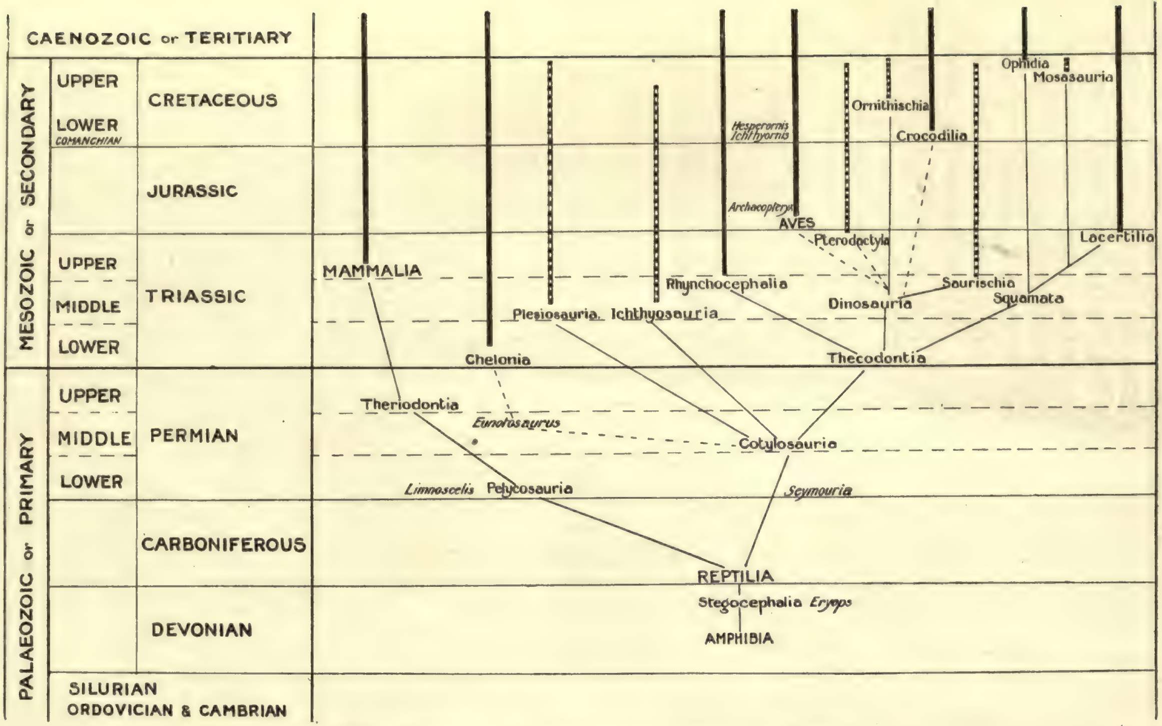


FIG. 166.—Diagram to illustrate the history of the Reptilia.

Continuous wide black lines represent groups still living; interrupted wide lines represent groups that became extinct. Straight lines from name to name indicate generally accepted lines of descent; dotted lines, probable lines of descent. No attempt has been made to indicate the relative thicknesses of the layers.

years ago, and some think very much longer than this. These first quadrupeds were the Amphibia, swamp-dwelling creatures somewhat resembling the newts and salamanders of to-day, and from which the tailless forms like frogs and toads arose later. Towards the end of the Devonian period appeared a specialised group, the **Stegocephalia,** found all over Europe and North America. To this belonged a form termed *Eryops*, which, while appearing at a somewhat later time, is interesting, since it is but little specialised, and from similar forms the early reptiles could have arisen. In appearance it is not unlike a large newt, although its skeleton and, in particular, its skull is of a more advanced type. The first true Reptiles made their appearance in the Carboniferous period, and by the end of it and the beginning of the Permian, we find them committed to at any rate two different lines of development, which we shall follow separately. The differences between these early Reptiles and the Amphibia are very slight, so that the line of demarcation between them is difficult to draw.

The first reptiles to notice are a group, the **Pelycosauria,** of world-

Fig. 167.—Restoration of the Permian reptile, *Limnoscelis paludis*, from New Mexico.—After a model by Lull.

wide distribution, and of which *Limnocelis* will serve as a little-specialised type. It is slightly more lizard-like than *Eryops*, and more adapted for life on dry land. As a rule, the members of this group remained little modified, but certain forms like *Edaphosaurus* and its allies had the neural spines of the vertebræ enormously elongated and a large web-like extension of the skin between them. These strange forms rarely exceeded a length of 5 feet, and soon died out. From the Pelycosauria were derived a second group, the **Theriodontia,** or reptiles with mammal-like teeth, first appearing in Upper Permian beds in South Africa. They are far more adapted to life on land, and progressed fairly rapidly, holding their bodies well up off the ground and running like a mammal instead of crawling like a lizard. From this group in the Triassic period arose the primitive Mammalia, whose remains have been found in the upper strata of this series in South Africa. Thus we have derived from the one specialisation of the early Reptiles, the Mammals, a group destined to spread over the whole world, to become adapted to

various conditions of life, and, finally, to become a dominant class culminating in Man himself. Lack of space prohibits more than this brief indication of their line of origin.

To pass back to the second group of primitive reptiles, we find in early Permian times a form termed *Seymouria*. This is a slightly stouter animal than *Eryops*, exhibiting many Stegocephalian features, but showing a certain approach towards the higher Reptilia. It may be considered as a lowly representative of a diversified group of primitive Reptiles, the **Cotylosauria,** from which

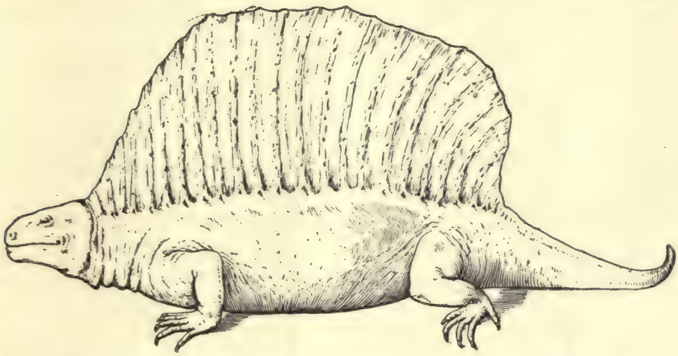


FIG. 168.—Ship-lizard, *Edaphosaurus cruciber*, Permo-Carboniferous, North America.—After Case.

the higher forms originated, and which was duly established by the end of the lower Permian. At any rate, three, or perhaps four, distinct lines of development from this group can be traced. The Cotylosaurs were land dwellers, but from time to time some of their descendants returned again to the sea. The first line we shall notice is but little known, and culminated in the Turtles and Tortoises, or **Chelonia,** as they are collectively termed. They first make their appearance in early Triassic times as quite highly specialised forms, easily recognisable as similar to their descendants living to-day. They are characterised by the broadening and flattening of their ribs and the development of a characteristic box-like skeleton. Of their previous history but little is known, save for an interesting form, *Eunotosaurus*, from the late middle Permian beds, an animal with broad expanded ribs and a peculiar skull that is regarded by some authorities as a form linking the Chelonia with the Cotylosaurs. The second line is the **Plesiosauria,** large aquatic lizards that make their appearance in Mid Triassic times. Their remains are probably the most widely spread and common of all fossils, being recorded from all parts of the world. Of the hundreds of skeletons known

some are almost complete and beautifully preserved. They varied considerably in size, but were practically all large, ranging from about 10 up to 50 feet in length. The body was stout and the limbs transformed into two parts of large powerful paddles; the tail was fairly short, the neck long, and the mouth armed with formidable teeth. In the case of *Elasmosaurus*, the neck reached a

Fig. 169.—Plesiosaur, *Cryptocleidus*, restored by Knight.

length of 23 feet out of a total of 41 feet. The third line, the **Icthyosauria,** also appearing in Mid Triassic strata, were also aquatic, large in size, widespread, and again, have left some remarkably well-preserved skeletons. These were more like fish or, rather, dolphins in body form than the previous group, and swam vigorously by means of a powerful tail. The limbs are not so large, and apparently

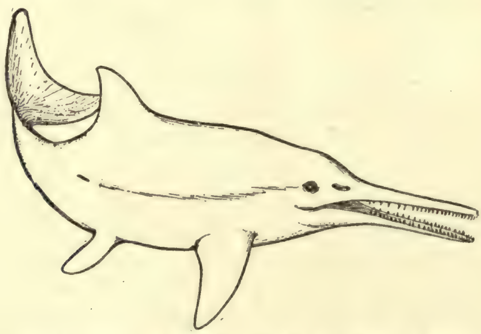


Fig. 170.—Ichthyosaur. Restoration by Knight.—From Schuchert's "Historical Geology."

acted in the manner of fins. The neck is quite short and the head pointed. They varied in size from 2 feet up to 30 feet, and possessed very large eyes. Often the remains of an adult are found accompanied by those of several young, so that the offspring apparently remained with the parents for some time. As noted above, the Plesiosaurs and Icthyosaurs were widely spread over the globe, and both groups died out in Cretaceous times; the latter disappearing in the middle strata and the former lasting on into the upper beds.

The fourth line of evolution is a very important one, since it led

to the groups ancestral to all modern Reptilia, except the Chelonia, and to Birds, as well as to the most extraordinary forms of Vertebrates that have lived on the Earth. They all probably originated from a group, the **Thecodontia,** first known from the Lower Trias. These were comparatively small, little specialised forms, showing certain advances over the Cotylosauria in the structure of the skull and shoulder girdle. From them sprang the **Squamata,** the **Dinosauria,** and, perhaps, also the **Rhynchocephalia.** The last group probably appeared in Mid Triassic times, and while resembling true Lizards in external appearance, they nevertheless present important points of difference from them in the characters of their skeleton, notably of the skull. They were apparently never a very extensive group, but one solitary member of it, the New Zealand Tuatara, *Sphenodon punctatus*, has persisted to the present day. It is now confined to certain islands off the coast of New Zealand, and is in grave danger of extinction at no very distant date. The Squamata also appear in the Mid Trias, and constitute the true Lizards and other allied forms derived from them. The term Lizard, as applied to living forms, is restricted to the Order **Lacertilia,** examples of which are first found in late Triassic times. They have persisted until to-day, and now form a fairly widespread group, the Lizards, Iguanas, Monitors, Blind-worms, etc., living in the temperate, subtropical, and tropical zones. On the whole, they are adapted for a life on dry land, many of them even to the desert, but some are burrowing forms and a few partly aquatic. From the Squamata, perhaps during the Upper Trias, were derived the snakes, or **Ophidia,** which still persist, although we find no record of them until the Upper Cretaceous. They also gave rise presumably about the same time to the **Mosasauria,** which were a group of aquatic forms having but a relatively short existence, appearing first in the Upper Cretaceous and becoming extinct in the same period. In spite of their limited duration they were highly specialised, large in size, varying from 8–50 feet in length, and were widely scattered over the globe. They left well-preserved fossil remains, including in some cases pieces of skin, and from the fact that they had a powerful set of teeth, and their bones often bear healed scars, we may assume they were fierce fighters. In form they were somewhat eel-shaped, with limbs reduced to small fin-like structures and a powerful tail, which was not of the same fish-tail shape as in the Ichthyosaurs.

The **Dinosauria** are a large diverse group that were apparently the dominant land-dwelling Vertebrates throughout a large part of the Mesozoic era. They first appear in the Middle Trias, and show two distinct lines of development: the **Saurischia,** in which the bones of the pelvic girdle resemble those in Lizards, and

the **Ornithischia,** in which the girdle approaches more closely that of the birds. The Order **Crocodilia**—Crocodiles, Alligators, and Gavials—probably arose from the Saurischia in Mid Triassic times, but their remains are not found until the early layers of the

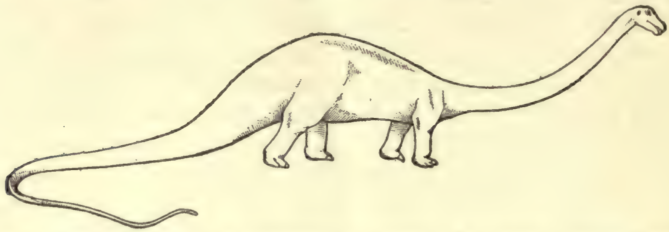


FIG. 171.—Restoration of the sauropod dinosaur, *Diplodocus*, based upon the mounted specimen in the Carnegie Museum. Length, 87 feet. Comanchian, Wyoming.—After Lull, from Schuchert's "Historical Geology."

Comanchian, when they are fully differentiated and resemble modern forms. Undoubted **Saurischian Dinosaurs** appear in the Upper Trias, and continue on until the end of the Cretaceous. They become specialised along two lines, the one herbivorous and

FIG. 172.—Restoration of *Brachiosaurus*, the most ponderous sauropod. Length, about 80 feet. Comanchian, North America and East Africa.—Modified from Matthew.

the other carnivorous. The herbivorous forms reached their zenith in the Comanchian times, when they were represented by three gigantic forms, *Diplodocus*, *Brontosaurus*, and *Brachiosaurus*, undoubtedly the largest land animals of which we have any knowledge. They were about 87 feet, 66 feet, and 80 feet long respectively,

but, in spite of its greater length, *Diplodocus* was not so huge an animal as *Brachiosaurus*, for while the former weighed about 30 tons, the latter was over 40, and *Brontosaurus* was intermediate between them. They were all apparently slow-moving swamp-dwellers, walking on all fours. They had long necks and tails, and very small heads compared with the bulk of the body. The carnivorous types culminated in *Tyrannosaurus*, which reached a length of 47 feet. It ran on its strong hind legs, and in this position its height was from 18–20 feet. Its head is about 4 feet long, very massive, and

FIG. 173.—Restoration of *Tyrannosaurus*, based upon a specimen in the American Museum of Natural History. Length, 47 feet. Cretaceous, western North America.—After Lull, from Schuchert's "Historical Geology."

provided with powerful teeth, so that altogether it was well fitted to prey on the large herbivorous forms.

The **Ornithischia** probably arose about the same time, or perhaps a little later, than the Saurischia, and they show three distinct lines of modification, and are remarkable not so much for their size as for the extraordinary and often bizarre form assumed by their armour. The first line led to swift-running forms, which were bird-footed and bipedal ; the second line produced forms with a great development of armour in the form of plates and spines ; and the third line is characterised by the development of horns and of a large bony neck frill. The two last groups were quadrupedal. The bird-like forms are represented by a number of animals like *Iguanodon*, from the Cretaceous beds of Belgium and the Isle of Wight. This was a large creature about 34 feet long with very powerful hind limbs, and the hand bore a very well-marked spine-like thumb. The most striking of the armoured Dinosaurs is perhaps *Stegosaurus*, which reached a length of about 20 feet. Along each side of its

back was a row of great upstanding plates, and on the tail four pairs

FIG. 174.—Restoration of *Iguanodon*. Cretaceous of Belgium and the Isle of Wight.—After Heilmann.

of powerful spines 2 feet or more in length. It is also noteworthy

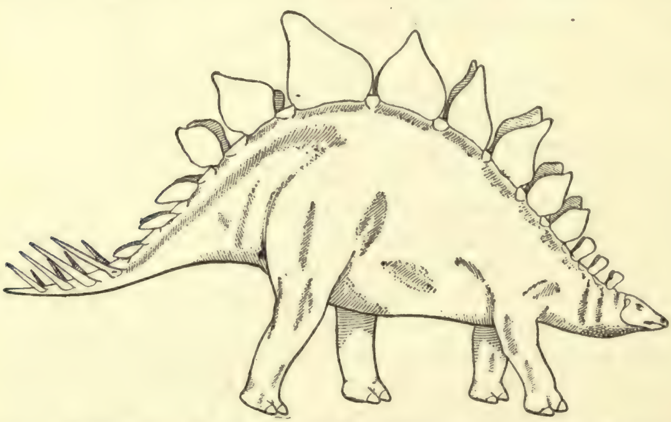


FIG. 175.—Restoration of the armoured dinosaur, *Stegosaurus*, based upon the mounted skeleton in the Yale University Museum. Length, about 20 feet. Comanchian, Wyoming and Colorado.—After Lull, from Schuchert's "Historical Geology."

in that its brain was extremely small, and it had a big swelling in

the lumbar region of the spinal cord many times larger than the brain, and presumably to look after the heavy hind limbs and tail. The horned forms are represented by such an animal as *Triceratops*, in form somewhat like a Rhinoceros, and reaching a length of 20–

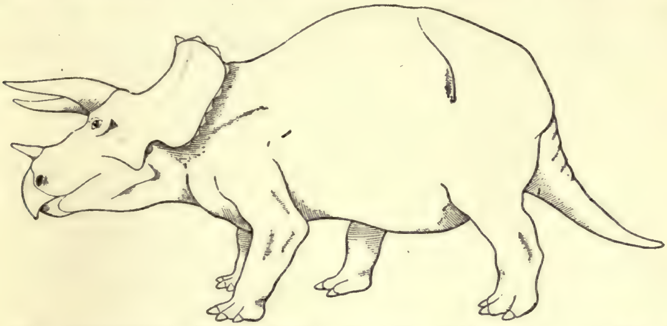


FIG. 176.—Restoration of the horned dinosaur *Triceratops*. Length, 20–25 feet. Upper Cretaceous (Lance), western North America.—After Lull, from Schuchert's "Historical Geology."

25 feet. It had a sort of short beak, two large horns over the eyes, one over the nasal region, and a large frill-like collar of bone extending back over the neck.

In early Jurassic times a remarkable group of flying lizards, the **Pterodactyla**, arose probably from the same group as the

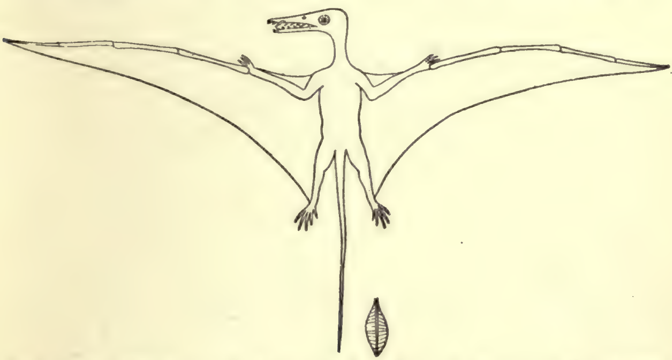


FIG. 177.—Pterodactyl, *Rhamphorhynchus phyllurus*.—After Lull.

Ornithischia, and persisted until the end of the Cretaceous. They were provided with wings, not produced, as in birds, by the development of feathers on the fore limb, but by the growth of a membrane stretching from the tips of the enormously elongated fingers back to the toes, and so somewhat similar to the bats of to-day. Their heads

were fairly large, and the strong jaws were well armed with teeth. While some of them were no larger than a sparrow, others reached a large size, even as much as 27 feet across the wings, and so they must have presented a truly terrific aspect well justifying their popular name of "flying dragons."

Again, the common Ornithischian stock probably gave rise to the true birds. The forerunner of the **Class Aves** was a remarkable

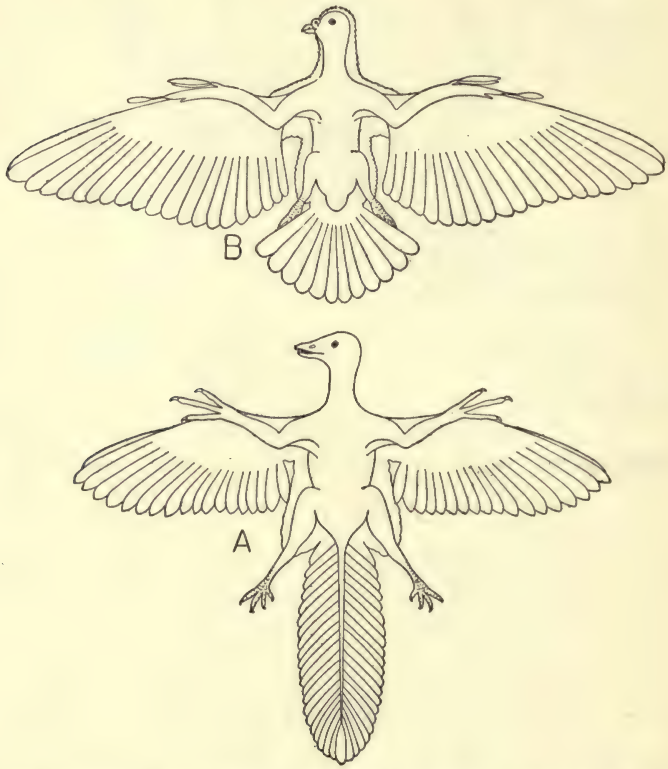


FIG. 178.—Reptilian bird, *Archæopteryx* (A), compared with pigeon, *Columba livia* (B).—After Lull.

creature that is found in early Jurassic times and known as *Archæopteryx*. Two fairly complete skeletons of this animal are known, but we have no indication of its exact derivation. It was bird-like in many respects, such as the general shape of the body, the feet, and the possession of quite typical feathers and true wings. On the other hand, it had also distinct Dinosaur affinities, which mark it off sharply from modern birds. Thus it had a long pointed tail, short,

clawed fingers on the front of the wing, and jaws with a number of pointed teeth. Later, in Comanchian times, we encounter another bird group exemplified by *Ichthyornis* and *Hesperornis*. These were fairly typical water birds in general appearance, had shortish tails, and were covered with feathers. Their heads have certain reptilian resemblances, the jaws bore teeth, and the breast bone was not keeled. True birds appear in the Tertiary, and are closely related to living forms. In spite of the breaks in the record, however, there is little doubt about the general relationship of true birds with their precursors.

We have thus in a very superficial manner touched on some of the main types of the Reptilia, indicated the important lines of evolution they followed, and shown their relation to the animals living to-day. Only a few of the striking forms have been mentioned and many more are known. As a class they spread widely over the surface of the earth, and were so plentiful and diverse in the Mesozoic times that we often refer to this period as the "Age of Reptiles." As to the reasons for the decline of the Reptiles, the times in which they lived are so remote that they become matters of conjecture, but certain points seem to stand out fairly clearly. The greater part of the Mesozoic was a period of relative stability, or of only very gradual change, so that many groups of the Reptiles were able to branch out and become highly adapted to certain environments. The close of the era was marked by very far-reaching and profound changes in the configuration of the land surface. These were probably accompanied also by considerable climatic alterations. The result was, that the highly modified forms had, as the very outcome of this specialisation, apparently lost the power to become re-adapted to altered environmental conditions. Thus during this transition time the Ichthyosaurs, Plesiosaurs, Mosasaurs, Pterodactyls, and both groups of the Dinosaurs, died out in the Middle and Upper Cretaceous times. This left a number of forms which were either little specialised as the early Mammals, Crocodiles, and Lacertilia, and capable of giving rise to new diversity, or else, like the Aves and Chelonia, capable of becoming adapted to the changed conditions. It seems probable, then, that the end of the dominance of the Reptiles was the result, direct or indirect, of changed environment.

The history of the Reptiles serves to illustrate the general course of evolution in the animal kingdom in general. In the first place, we have seen lowly little specialised forms branching out into various modes of living, and becoming fitted for life in various environments. That is to say, the generalised type spreads out into a series of adaptive specialisations that produce a diversity of forms, and we may say that, on the whole, groups of animals have

followed this process of **"Divergent Evolution."** They tend to diverge more and more from one another and from the ancestral stock as evolution proceeds, and we can express their inter-relations schematically in a branched fan-like diagram.

Looked at from another point of view, we may regard it as an illustration of what has been termed **"Adaptive Radiation."** That is to say, when a form or type of animal organisation has been established, its descendants proceed to spread out and become adapted to a number of different environments : the air, the sea, the swamp, the forest, the arid plain, and so on. Any line may become highly adaptive, possessing remarkable peculiarities, yet each group retains certain characters, not the same in each case, of course, reminiscent of the ancestral form.

Another phenomenon not nearly so widespread as divergence, but, nevertheless, of considerable importance, may also be noted. It follows as a result from this adaptive radiation that takes place in various groups. Members of various and quitc different groups may take to living in almost identical environments, say, for example, the air or the sea. If it is an environment that demands a high degree of specialisation in order to bring about satisfactory adaptation, as both of these do, then we sometimes find animals of quite different groups assuming forms with a greater or less amount of superficial resemblance. Thus, for example, we find birds, bats, and pterodactyls, while not at all closely related, live in the same environment and exhibit obvious similarities, particularly the last two. Again, there is a strong resemblance between Fish, Ichthyosaurs, Mosasaurs, Dolphins, and Whales, and in the case of the limbless lizards, *e.g.* Blind-worms and Snakes, the approach is very striking. To this we apply the term **"Convergent Evolution"** or **"Parallelism in Evolution."** In classifying animals it is obvious that this convergence must be taken into account, or otherwise we should be liable to group together erroneously animals whose similarities are due to their being adapted to a similar environment, and not to a community of descent.

Here the above outline of some of the main problems that arise from a consideration of Evolution, Variation, and Heredity may be brought to a conclusion. It is not intended to imply that there are no further problems to be studied, but this chapter does not aim at being even a statement of all the various biological theories, which would in itself require a volume many times larger than this. Rather has it attempted to indicate certain outstanding points and to provide an introduction to further and wider reading in these matters in which many excellent texts are now available.

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